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## THE MANIFESTATIONS OF THE PRINCIPLES OF CHEMICAL MECHANICS IN THE LIVING PLANT.<sup>1</sup>

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### THE UNIFORMITY OF NATURE.

Among the phenomena of nature man finds himself to be one of medium magnitude, for while his dimensions are about a billion times as great as those of the smallest atoms that compose him they are also about one billionth part of his distance from the center of his solar system.

From the vantage point of this medium magnitude the man of science scans eagerly the whole range of natural phenomena accessible to him with a strenuous desire for unity and simplification.

By the unwearying study of special sections of this long front of natural phenomena special guiding principles have been detected at work locally. No sooner has this been accomplished than, in obedience to this desire for continuity throughout, such principles have been freely extended on either side from the point of discovery.

Thus, the theory of probability, which dealt at first with so limited an occupation as drawing white and black balls out of an opaque bag, now is known as the only determinable factor in such remote things as the distribution of the duration of human lives and the effect of concentration of the colliding molecules in a solution upon the rate of their chemical change. Again, the principle of evolution discovered among living things has been

<sup>1</sup> Address of the president of the Botanical Section of the British Association for the Advancement of Science. Dublin, 1908.

extended, till to speak of the evolution of societies, of solar systems, or of chemical elements is now but commonplace.

The biologist, with all his special difficulties, has at least the limitation that he is only concerned with the middle range of the interminable hostile front of natural phenomena, and that for him is ordained the stubborn direct attack, leaving the brilliant attempts at outflanking movements to the astronomers on the one wing and the workers at corpuscular emanations on the other.

The atoms and molecules that the biologist has to deal with do not differ from those passing by the same names in the laboratories of chemistry and physics (at least no one suggests this), and their study may therefore be left to others. At the other end of the scale, with astronomical magnitudes we have not to deal, unless indeed we yield to the popular clamour to take over the canals on Mars as phenomena necessarily of biological causation.

In the study of that particular range of phenomena which is the special allotment of the physiologists, animal and vegetable, we have had ever before us the problem of whether there is not here some discontinuity in nature; whether the play of molecular and atomic forces occurring outside the living organism can ever account for the whole of the complexity and correlation of chemical and physical interactions demonstrable within the living structure.

As yet we are of course far from any answer to this question, and no one in a scientific assembly like this will call upon us for prophecies. Yet the subject to which I shall devote my address has a bearing upon this question. I propose to consider a particular aspect of the relation of chemical changes in a test-tube to those taking place in a living growing plant, and this in the spirit of one who craves for continuity throughout natural phenomena.

The point of view from which the chemist regards the reaction taking place in his test-tube has undergone a

change in the last twenty years, a change bringing it more into uniformity with that of the biologist. No longer content with an equation as a final and full expression of a given reaction, the chemist now studies with minutest detail and with quantitative accuracy the progressive stages of development of the reaction<sup>2</sup> and the effect upon it of varied external conditions, of light, temperature, dilution, and the presence of traces of foreign substances.

Perhaps it is too much to believe that this, as it were physiological, study of each reaction is the effect of some benign irradiation from the biological laboratory. At least, however, it is true that it is the modern study of "slow" chemical reactions which has made all this possible, and the living organism consists almost entirely of slow reactions. The earliest studied chemical reactions, those between substances which interact so quickly that no intermediate investigation can be made, did not of course lend themselves to this work, but nowadays whole classes of reactions are known which are only completed hours or days after the substances are initially mixed. To the slow reactions belong all the hydrolytic and dehydration changes of carbohydrates, fats and proteids that bulk so largely in the metabolism of plants and animals, together with other fermentation changes such as are brought about by oxidases, zymases and enzymes in general. This precise quantitative study of chemical reactions has been developing with remarkable acceleration for some twenty-five years, till it is grown almost into an independent branch of science, physical chemistry. This is sometimes called "general chemistry" because its subject is really the fundamental universal laws of the rate of chemical change, and these laws hold through all the families, genera and species of chemical compounds, just as the same physiological laws apply to all the different types of plants.

<sup>2</sup> Modern research has made it clear that reactions conventionally represented by complex equations of many interacting molecules really take place in a succession of simple stages, in each of which, perhaps, only two molecules interact.

Now if these laws are fundamental with all kinds of chemical change they must be at work in the living metabolic changes. If the chemical changes associated with *protoplasm* have any important factor or condition *quite different* from the state of things which holds when molecules react in aqueous solution in a test-tube, then it might happen that the operation of these principles of physical chemistry would be obscured and not very significant, though it is inconceivable that they should be really inoperative.

My present intention, then, is to examine the general phenomena of metabolism in an attempt to see whether the operations of these quantitative principles are traceable, and if so how far they are instrumental in giving a clearer insight into vital complexity.

#### THE DOMINANCE OF IRRITABILITY IN PHYSIOLOGY.

I think that certain manifestations of these principles are indeed quite clear, though not generally recognized, and that this neglect is largely due to the dominance of what our German colleagues call "*Reizphysiologie*"—the notion that *every* change in which protoplasm takes part is a case of the "*reaction*" of an "*irritable*" living substance to a "*stimulus*." Now this general conception of protoplasmic irritability, of stimuli and reactions was, of course, a splendid advance, the early development and extension of which we owe largely to our veteran physiologist Professor Pfeffer, of Leipzig. Great as is the service it has rendered to many departments of botany, yet in one direction, I think, it has overflowed its legitimate bounds and swamped the development of the physical-chemical concepts which I shall indicate later on. The great merit of the "*stimulus and reaction*" conception is that it supplies a very elastic general formula for the sort of causal connection that we find occurring in all departments of biology; a formula which allows the phenomena to be grouped, investigated and formally expounded, whether they be the temporary turgor-movements of "*sensitive*"

plants, the permanent growth movements of tropistic curvatures, or the complex changes of plant-form and development that result from present and past variations of external conditions.

The strength and the weakness of the conception lie in its extraordinary *lack of particularity*. When an irritable cell responds to a stimulus by a reaction nothing is implied about the mechanism connecting the *cause and the effect*, and nothing even about the relative magnitudes of these, but all this is left for special research on the case under consideration. The one natural chain of cause and effect that is recognized to be outside this comprehensive category is that rather uncommon one in which a definite amount of energy of one kind is turned into an equivalent definite amount of energy of another. Here we have a direct "equation of energy," whereas in a reaction to a stimulus we are said to have typically an "unloosing" effect—a liberation of potential energy by a small incidence of outside energy, as in the classical analogies, drawn from completely comprehended non-living things, of a cartridge exploded by a blow, or the liberation into action of a head of water by the turning of a tap.

So elastic a conception may be easily stretched to fit almost any sequence of phenomena with the apparent closeness that argues a bespoke garment. We must therefore be critically on our guard against cases of such sartorial illusion.

#### THE PRINCIPLES OF CHEMICAL MECHANICS.

That my consideration of particular cases may be intelligible it seems necessary that I devote a few minutes to outlining the four quantitative mechanical principles which govern every single chemical reaction, though much that I have to say has been drawn from elementary books on physical chemistry.

These four principles are concerned with (1) the nature of the reaction in question; (2) the amount of reacting substances that happen to be present; (3) the temperature

at which the reaction is taking place; and (4) the influence of catalysts upon the reaction.

For the moment we will confine ourselves to the first two matters, and assume that catalysts are absent and the substances at constant temperature.

1. The first principle that we have to consider is that which declares that no chemical reaction is really instantaneous, though the interaction of substances is often so fast that a direct measurement of its rate can not be made; and, further, that every reaction has its own *specific reaction-velocity* which distinguishes it from other reactions. This is expressed by giving to each particular reaction a numerical *velocity coefficient* which is low or high proportionally as the reaction is slow or quick.

2. This coefficient only expresses the actual experimental velocity when the reacting substances are present in *unit* concentration, because difference of concentration is just the most important factor controlling the actual reaction-velocity.

If a solution of a substance *A* of unit concentration is undergoing change, then to keep this reaction going at its present rate fresh amounts of *A* must be added continually just to equal the amount removed by the reaction and so keep the substance up to unit concentration. The amount of *A* that had to be added thus per unit time would give an exact measure of the amount being decomposed, *i. e.*, of the specific velocity of this reaction.

If the reaction were started with *A* at double unit concentration, then twice as much *A* would have to be added *per* unit time to keep the reaction velocity constant at the double rate it would have started at.

And with higher concentrations proportionally more *A* would have to be added. It is therefore shown that the amount of chemical change going on in unit time is proportional to the concentration. This is a most fundamental principle of chemical mechanics, known as the *law of mass*, and it may be stated thus: *the amount of chemical change taking place at any time is always propor-*

*tional to the amount of actively reacting substance (or substances) present.*

To carry out experiments by the procedure given above is in practise very difficult and the velocities of reactions are never measured by the chemist in this way. In a living organism this continual bringing up of new supplies of material to maintain a constant rate of change is the ordinary way of life, but in the chemical laboratory procedure is different. There, definite amounts of substances are initially mixed in a vessel and the reaction is allowed to progress by itself without further additions. In this case there is a continual falling off of the concentration of the substance, and so a corresponding diminution of the actual reaction-velocity.

In this procedure the diminution of the initial amount of substance can be actually measured by withdrawing small samples at intervals of time and analyzing them. Let us consider a definite example. Cane-sugar can be hydrolyzed, under various conditions, to give two molecules of hexose, according to the equation



This reaction goes on, though extremely slowly, when an aqueous solution of cane-sugar is kept very hot in a beaker. Suppose we started with, say 128 grams dissolved in a liter of water and traced the diminution of this amount down towards zero by withdrawing samples at intervals of time and analyzing them. If we plotted the sugar-content of these successive samples against the times when they were taken we should get the curve given in Fig. 1. If we call  $n$  minutes the time taken for the sugar to diminish from 128 grams to 64 grams, we should find that in the second  $n$  minutes the sugar had fallen to 32 grams, after  $3n$  minutes to 16 grams, and so on, the amount halving itself every  $n$  minutes. Thus the amounts of cane-sugar hydrolyzed in successive equal intervals are 64, 32, 16, 8, 4, 2, 1 grams, amounts in each case just exactly proportional to the quantity of

cane-sugar then remaining in solution, thus exemplifying the law of mass.

Such a curve as *A* in Fig. 1, which changes by a constant multiple for successive units of time (here halving itself every *n* minutes) is known as a logarithmic curve; the velocity of reaction at any moment is exactly indicated by the steepness of the curve at that moment; the velocity is greatest at first and it declines to almost zero as the curve approaches the horizontal at the end of the reaction.

When instead of the decomposition of a single substance we deal with two dissolved substances, *A* and *B*, reacting together, then as *both* of them go on being thus used up, the amount of change must be ever proportional to the mass or amount of *A* present multiplied by the mass of *B* present.

There is a special important case when the amount of, say, *B* is in very great excess of that amount required to unite with the whole of *A*. Then all through the slow progress of the reaction the amount of *B* never becomes reduced enough to make appreciable difference to its mass, and it may be considered as practically constant all along. In such a case the rate of the reaction is found to be proportional simply to the amount of *A* present, and we get again the curve *A*, Fig. 1. Here the amount of *A* may be considered as a limiting factor to the amount of reaction; *B* being in such great excess never falls low enough to take a practical part in determining the velocity.

The case of the hydrolysis of cane-sugar in aqueous solution is just such a case. The water itself enters into the reaction, but so little is used up in relation to the enormous excess present that the amount remains practically constant and the rate of hydrolysis of the cane-sugar is determined only by the amount of the cane-sugar present at any moment.<sup>3</sup>

3. We have now shown how the actual amount of chemical change going on in a solution is determined by the

<sup>3</sup> 128 grams cane-sugar unite with 6.7 grams water in hydrolysis, and in our experiment nearly 1,000 grams of water are present.

combined effect of (1) the specific reaction velocity and (2) the law of mass. We have next to point out that the specific reaction coefficient is not the same under all circumstances, but is affected by variations of external conditions, always by temperature, and generally by the presence of traces of so-called catalysts.

The relation to temperature we will postpone, and proceed to consider our third principle, the acceleration of reaction velocity by *catalytic agents*.

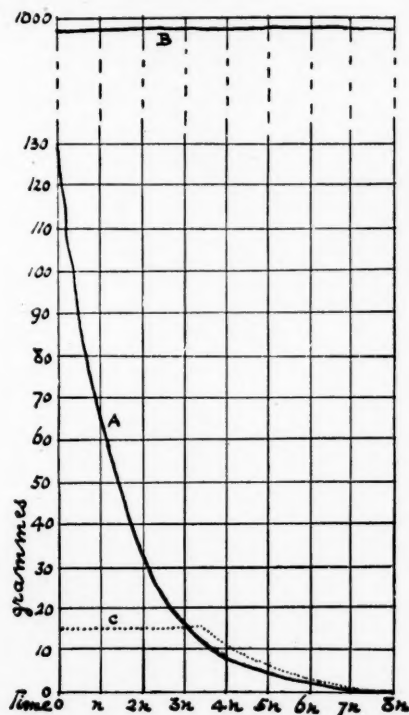


FIG. 1.

It has long been known that small additions of various foreign substances may have a great effect in increasing the rate at which a reaction is proceeding. Thus this hydrolysis of cane-sugar, so slow with pure water, goes at a

fair velocity if a few drops of a mineral acid are added to the solution, while the addition of a trace of a particular enzyme (invertase from plant or animal) enormously increases the rate of change, so that the whole 128 grams of cane-sugar are soon hydrolyzed to hexose. The reaction progresses quantitatively in the same sort of way as before, giving a logarithmic curve of sugar-content. Indeed the same graphic curve, Fig. 1, *A*, would represent the facts if the value of *n* were reduced from many hundred minutes to quite a few.

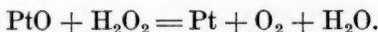
The most striking point about this new state of things is that the added body is not used by its action, but the acid or enzyme is still present in undiminished amount when the reaction is completed.

Such actions were at first styled "contact" actions, but are now known as catalytic actions, because we have learned that the catalyst does not work just by contact but by combining with the sugar to form an intermediate addition compound, and that this compound is then split up by the water liberating the catalyst again, but freeing the sugar part, not as cane-sugar, but combined with the water to form two molecules of hexose.

On many chemical reactions, finely divided metals such as platinum and gold have a very powerful catalytic action. Thus platinum will cause gaseous hydrogen and oxygen to unite at ordinary temperatures, and will split up hydrogen dioxide with the formation of oxygen. The intermediate stages in this catalytic decomposition may be summarily simplified to this—



and



Thus the reaction goes on and on by the aid of the appearing and disappearing "intermediate compound" PtO till at the end the  $\text{H}_2\text{O}_2$  is all decomposed and the platinum is still present unaffected.

The enzymes are the most powerful catalytic agents

known, and most of them are specifically constituted to effect the hydrolysis, oxidation, reduction or splitting of some definite organic compound or group of compounds containing similar radicals.

Innumerable enzymes have in late years been isolated from the plant-body, so that it would seem that there is none present to catalytically accelerate each of the slow single changes that in the aggregate make up the complex metabolism of the plant.

The law of mass applies with equal cogency to *catalytic* reactions. If twice the amount of acid is added to a solution of cane-sugar (or twice the amount of enzyme) then the reaction velocity is doubled, and hydrolysis proceeds twice as fast. As the catalyst is not destroyed by its action, but is continually being set free again, the concentration of the catalyst remains the same throughout the reaction; while, on the contrary, the amount of cane sugar continually decreases.

If the catalyst be present in great excess the amount of hydrolysis will be limited by the amount of cane-sugar present, and as this is used up so the reaction will progress by a logarithmic curve as in Fig. 1, *A*. In this case *B* may represent the amount of catalyst. If, on the contrary, there is a large amount of sugar and very little acid or enzyme present, so that the catalyst becomes the limiting factor, then we happen upon a novel state of things; for by the law of mass the rate of hydrolysis will now remain constant for some time till the excess of sugar is so far reduced that it in turn becomes a limiting factor to the rate of change. In this case the velocity curve would consist of a first phase with a straight horizontal line of uniform reaction-velocity leading into the second phase of a typical falling logarithmic curve (see Fig. 1, *C*). These conditions have been experimentally examined by Horace Brown and Glendinning, and fully explained and expounded by E. F. Armstrong in Part II of the critical "Studies in Enzyme Action."<sup>4</sup>

<sup>4</sup> *Proc. Roy. Soc., Vol. LXXIII, 1904, p. 511.*

Having now outlined the three fundamental principles of reaction-velocity, the law of mass, and the catalytic acceleration of reaction-velocity, we are in a position to consider the broad phenomena of metabolism or chemical change in the living organism from the point of view of these principles of chemical mechanics.

THE METABOLISM OF THE PLANT CONSIDERED AS A CATALYTIC REACTION.

Plants of all grades of morphological complexity, from bacteria to dicotyledons, have this in common, that throughout their active life they are continually growing. Putting aside the *qualitative* distribution of growth that determines the morphological form, as a stratum of phenomena above the fundamental one that we are about to discuss, we find that this growth consists in the assimilation of dead food-constituents by the protoplasm with a resulting increase in the living protoplasm accompanied with the continual new formation of dead constituents, gaseous  $\text{CO}_2$ , liquid water, solid cellulose, and what not. This continual flux of anabolism and katabolism is the essential character of metabolism, but withal the protoplasm increases in amount by the excess of anabolism over katabolism.

Protoplasm has essentially the same chemical composition everywhere, and in the whole range of green plants the same food-materials seem to be required; the six elements of which proteids are built are obviously essential in quantity as building material, but in addition small amounts of Fe, Ca, K, Mg, Na, Cl and Si are in some other way equally essential. What part these secondary elements play is still largely a matter of hypothesis.

Regarding metabolism thus crudely as if it were merely a congeries of slow chemical reactions, let us see how far it conforms to the laws of chemical mechanics we have outlined.

If the supply of any one of these essential elements comes to an end, growth simply ceases and the plant

remains stationary, half-developed. If a *Tropæolum* in a pot be watered with dilute salt-solution, its stomata soon close permanently, and no  $\text{CO}_2$  can diffuse in to supply the carbon for further growth of the plant. In such a condition the plant may remain for weeks looking quite healthy, but its growth may be quite in abeyance.

In agricultural experience, in manuring the soil with nitrogen and the essential secondary elements, the same phenomenon is observed when there is a shortage of any single element. If a continuous though inadequate supply of some one element is available then the crop development is limited to the amount of growth corresponding to this supply. Agriculturalists have formulated the "law of the minimum," which states that the crop developed is limited by the element which is minimal, *i. e.*, most in deficit. Development arrested by "nitrogen-hunger" is perhaps the commonest form of this. All this is of course in accordance with expectation on physical-chemical principles. The quantity of anabolic reaction taking place should be proportional to the amount of actively reacting substances present, and if any one essential substance is quite absent the whole reaction must cease. It therefore seems clouding a simple issue and misleading to say of a plant which, from the arrested development of nitrogen-hunger, starts growth again when newly supplied with nitrogen, that this new growth is a response to a "*nitrogen stimulus*." It would appear rather to be only the removal of a limiting condition.

Let us now move on a stage. Suppose a growing plant be liberally supplied with all the thirteen elements that it requires, what, then, will limit its rate of growth? Fairy bean-stalks that grow to the heavens in a night elude the modern investigator, though some hope soon to bring back that golden age with overhead electric wires and underground bacterial inoculations. If everything is supplied, the metabolism should now go on at its highest level, and quantities of carbon, nitrogen, hydrogen and oxygen supplied as  $\text{CO}_2$ , nitrates and water will interact so that these

elements become converted into proteid, cellulose, etc. Now this complex reaction of metabolism only takes place in the presence of protoplasm, and a small amount of protoplasm is capable of carrying out a considerable amount of metabolic change, remaining itself undestroyed. We are thus led to formulate the idea that metabolism is essentially a catalytic process. In support of this we know that many of the inherent parts of the protoplasmic complex are catalytic enzymes, for these can be separated out of the protoplasm, often simply by high mechanical pressure. We know, too, nowadays that the same enzymes that accelerate katabolic processes also accelerate the reverse anabolic processes.

In time a small mass of protoplasm will, while remaining itself unchanged, convert many times its own weight of carbon from, let us say, the formaldehyde ( $\text{HCHO}$ ) of photosynthesis to the carbon dioxide ( $\text{CO}_2$ ) of respiration.

If metabolism is a complex of upgrade and downgrade changes catalyzed by protoplasm we must expect the amount of metabolism to obey the law of mass and to be proportional to the masses of substances entering into the reaction. The case when any one essential element is a limiting factor we have already considered. When all are in excess, then the *amount of the catalyst present* becomes in its turn the limiting factor. Transferring this point of view to the growing plant, we expect to find the limited mass of protoplasm and its constituent catalysts setting a limit to the rate of metabolic change in the extreme case where all the materials entering into the reaction are in excess. When once this supply is available further increase in supplies can not be expected to accelerate the rate of growth and metabolism beyond the limit set by the mass of protoplasm. This, of course, is in accordance with common experience. The clearest experimental evidence is in connection with respiration and the supply of carbohydrates—this, no doubt, because the carbohydrate material oxidized in respiration is normally stored inside plant-cells in quantity and can be estimated. When the

supplies for an internal process have to be obtained from outside, then we have the complications of absorption and translocation to obscure the issue, especially in the case of a higher plant.

Let us first take a case where the carbohydrate supply is in excess and the amount of catalytic protoplasm is small and increasing. Thus it is in seeds germinating in the dark: respiration increases day by day for a time, though carbohydrate reserves are steadily decreasing. Palladine<sup>5</sup> has investigated germinating wheat by analyzing the seedlings and determining the increase of the essential (non-digestible) proteids day by day. The amount of these proteids he regards as a measure of the amount of actual protoplasm present. Assuming this to be so, he finds an approximately constant ratio between the amount of protoplasm at any stage and the respiration.

As germination progresses in the dark the supplies of reserve carbohydrate presently fail, and then the respiration no longer increases in spite of the abundant protoplasm. According to our thesis the catalyst is now in excess and the  $\text{CO}_2$  production is limited by the shortage of respirable material.

This second type of case was more completely investigated by Miss Matthæi and myself in working on the respiration of cut leaves of cherry-laurel kept starved in the dark. For a time the  $\text{CO}_2$  production of these non-growing structures remains uniform, and then it begins to fall off in a logarithmic curve, so that the course of respiration is just like *C* in Fig. 1. We interpret both phenomena in the same way: in the initial level phase the respirable material in the leaf is in excess, and the amount of catalytic protoplasm limits the respiration to the normal biological level; in the second falling phase some supply of material is being exhausted, and we get a logarithmic curve controlled by the law of mass, as much, it would seem, as when cane-sugar is hydrolyzed in aqueous solution.

After these two illustrations of the action of the law

<sup>5</sup> *Revue gén. de botanique*, Tome VIII, 1896.

of mass from the more simple case of respiration we return to the consideration of the totality of metabolic reactions as exemplified in growth.

What should we expect to be the ideal course of growth, that is, the increase of the mass of the plant regarded as a complex of reactions catalyzed by protoplasm? Let us consider, first, the simplest possible case, that of a bacterium growing normally in a rich culture solution. When its mass has increased by anabolism of the food material of the culture medium to a certain amount it divides into two. As all the individuals are alike, counting them would take the place of weighing their mass. The simplest expectation would be that, under uniform conditions, growth and division would succeed each other with monotonous regularity, and so the number or mass of bacteria present would double itself every  $n$  minutes. This may be accepted as the ideal condition.

The following actual experiment may be quoted to show that for a time the ideal rate of growth is maintained, and that at the end of every  $n$  minutes there is a doubled amount of protoplasm capable of catalyzing a doubled amount of chemical change and carrying on a doubled growth and development.

From a culture of *Bacillus typhosus* in broth at 37° C. five small samples were withdrawn at intervals of an hour, and the number of bacteria per unit volume determined by the usual procedure. The number of organisms per drop increased in the following series: 6.7, 14.4, 33.1, 70.1, 161.0.<sup>6</sup> This shows a doubling of the mass of bacteria in every fifty-four minutes and is the case actually represented in the strictly logarithmic curve of Fig. 2.

We may quote some observations made by E. Buchner<sup>7</sup> of the rate at which bacteria increase in culture media. *Bacillus coli communis* was grown at 37° C. for two to

<sup>7</sup> Buchner. Zuwachsgrossen u. Wachstumsgeschwindigkeiten. Leipzig, 1901.

<sup>6</sup> For this unpublished experiment on bacterial growth I am indebted to Miss Lane-Claypon of the Lister Institute of Preventive Medicine.

five hours, and by comparison of the initial and final numbers of bacteria the time required for doubling the mass was calculated. Out of twenty-seven similar experiments a few were erratic, but in twenty cases the time for doubling was between 19.4 and 24.8 minutes, giving a mean of 22 minutes. This produces an increase from 170 to 288,000 in four hours. No possible culture medium will provide for prolonged multiplication of bacteria at these rates.

Cohn<sup>8</sup> states that if division takes place every sixteen minutes then in twenty-four hours a single bacterium  $1\ \mu$  long will be represented by a multitude so large that it requires twenty-eight figures to express it, and placed end to end they would stretch so far that a ray of light to travel from one end to the other would take 100,000 years. The potentialities of protoplasmic catalysis are thus made clear, but the actualities are speedily cut short by limiting factors.

For a while, however, this ideal rate of growth is maintained. At the end of every  $n$  minutes there is a doubled amount of protoplasm present, and this will be capable of catalyzing twice the amount of chemical change and carrying on a doubled amount of growth and development. This is what common sense and the law of mass alike indicate, and is exactly what this logarithmic curve in Fig. 2 expresses.

This increase of the amount of catalytic protoplasm by its own catalytic activity is an interesting phenomenon. In Section K we call it growth, attribute it to a spe-

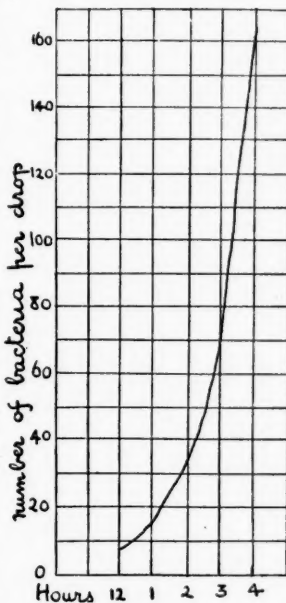


FIG. 2.

<sup>8</sup> Cohn. *Die Pflanze*. Breslau, 1882, p. 438.

cific power of protoplasm for assimilation (in the strict sense), and leave it alone as a fundamental phenomenon, but are much concerned as to the distribution of the new growth in innumerable specifically distinct forms. In the Chemical Section they call this class of phenomenon "autocatalysis," and a number of cases of it are known. In these a chemical reaction gives rise to some substance which happens to catalyze the particular reaction itself, so that it goes on and on with ever-increasing velocity. Thus, we said that free acid was a catalyst to the hydrolysis of cane-sugar; suppose now that free acid were one of the products of the hydrolysis of sugar, then the catalyst would continually increase in amount in the test-tube, and the reaction would go faster and faster. Under certain conditions this actually happens. Again, when methyl acetate is hydrolyzed we normally get methyl alcohol and free acetic acid. This free acid acts as a catalyst to the hydrolysis, and the rate of change continually accelerates. Here, if the supply of methyl acetate were kept up by constant additions, the reaction would go faster and faster with a logarithmic acceleration giving a curve of velocity identical with Fig. 2, *A*.

For a clear manifestation of this autocatalytic increase in the plant it is, of course, essential that the supply of food materials to the protoplasm be adequate.

Another case where we might look for a simple form of this autocatalytic increase in the rate of conversion of food materials to anabolites would be in the growth of a filamentous alga, like *Spirogyra*. Here, as in the bacterium, all the cells are still capable of growth. In this case the food-material needed in greatest bulk is carbon, which has to be obtained by photosynthesis. Some experiments have been started in the Cambridge Laboratory on the rate of growth of *Spirogyra* in large tubs of water kept at different temperatures and with varying facilities for photosynthesis and metabolism. Under rather depressing conditions the *Spirogyra* took several days to double its weight—a rate of metabolism out of all comparison slower than that of bacteria. Experiments on these

lines, with the different food materials as limiting factors, should give instructive results.

We turn now to consider the growth of a flowering plant. Here conditions are more complex, and we know that at the flowering stage or end of the season the growth diminishes considerably. This difference from a simple alga or bacterium we can only regard as a secondary acquisition in relation to the external conditions—either a reaction to a present external stimulus or to the memory of past stimuli. In a flowering plant, too, all the cells do not continue to grow; many cells differentiate and cease to grow and also some of the groups of meristem remain dormant in axillary buds. Clearly the growth curve can not continue to accelerate logarithmically, and in later phases it must tail off; the “grand period” which growth is said to exhibit is another way of stating this. It will, however, be of great interest to us to see what will be the form of the curve of growth during the early period of development.

The importance of this class of work has been realized in Geneva, and detailed work is now being done under the inspiration of Professor Chodat<sup>9</sup> in which the curve not only of growth (fresh weight) but of the uptake of all the separate important elements in selected plants is being carefully followed.

With plants grown in the open, climatic disturbances must occur. We shall therefore figure a curve for the fresh weight of a maize plant grown in water-culture. This is prior to the Geneva work, and due to Mlle. Stefanowska,<sup>10</sup> who has studied also the growth-curves of small animals. The first phase of the curve, lasting some fifty days, shows strictly uniform acceleration, doubling

<sup>9</sup> Monnier, A. *Les matières minérales et la loi d'accroissement des végétaux*. Geneva, 1905.

Déléano, N. *Le rôle et la fonction des sels minéraux dans la vie de la plante*. Geneva, 1907.

See also the independent work of Tribot. *Comptes rendus de l'Acad. des Sciences*, October 14, 1907.

<sup>10</sup> Stefanowska. *Comptes rendus de l'Acad. des Sciences*, February 1, 1904.

the weight of the plant every ten days (Fig. 3). The precise external conditions are not stated.

In spite of the morphological complexity the autocatalytic reaction of growth is apparently not checked by inadequate supplies before the plant enters rather suddenly upon the second phase. Here, from the present point of view, we consider that the progress of growth is interrupted, not by the primary physical-chemical causes, but by secondary causes, presumably to be classed in the category of stimulus and reaction.

The numerous curves for the accumulation of different organic and mineral constituents worked out for barley

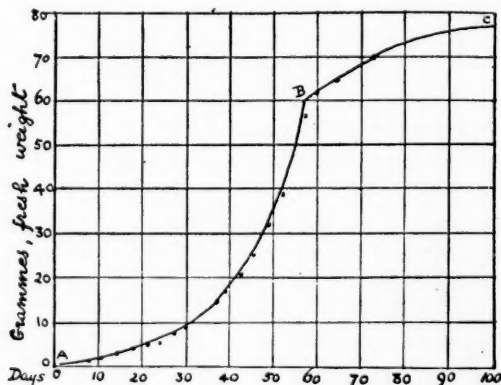


FIG. 3.

and buckwheat at Geneva are of similar form, but do not keep up the uniform rate of doubling so well as does the curve of total fresh weight.

In this connection the tall and dwarf forms of the same plant present an interesting problem, and some experiments have been started on sweet peas at Cambridge. At the time of germination the seedlings weigh about the same, whereas at the end of the season the weight of a tall plant is many times that of a dwarf "cupid" growing alongside under similar conditions. Is the difference due to a less vigorous autocatalysis in the dwarf form, so that throughout its growth it takes a greater number

of days to double its weight? Construction of the curves of growth through the season will show whether it is this or some other alteration in the form of the curve.

I now propose to say a few words about one last point in connection with growth considered as a phenomenon of catalysis before passing on to deal with the effects of temperature.

Of the metallic elements that are essential for the growth of plants some occur in such minute quantities that one can only imagine their function is catalytic. If iron, for instance, played any part in metabolism which involved its being used up in any building material or by-product of metabolism, then a larger amount than actually suffices should be advantageous. If its function is catalytic the iron would go on acting indefinitely without being consumed, and so a minute trace might serve to carry out some essential, and even considerable, sub-section of metabolism.

Elements like manganese, magnesium and iron are often associated with non-vital catalytic action, and a preparation of iron has recently been quantitatively investigated which seems to have literally all the properties of an organic oxydase from plant tissues.<sup>11</sup>

As long ago as 1869 Raulin observed that traces of unessential salts, in particular those of zinc, added to the culture medium in which he grew the fungus *Sterigmato-cystis* caused a rapid acceleration of the growth rate. The time that the mycelium took to double its weight was now reduced to a half or even a third. This continued enormous effect of so small a trace of substance is possibly to be regarded as an added catalyst to the normal protoplasmic apparatus. This sort of effect is currently labeled "chemical stimulation" and has been interpreted as an attempt of the fungus to grow away from an unpleasant environment. To me it looks as if such chemical stimulation were really another example of the in-

<sup>11</sup> Wolff, J. Des peroxydiastases artificielles. *Comptes rendus de l'Acad. des Sciences*, June 9, 1908.

judicious extension of the concept of stimulus and reaction.

This effect of zinc upon the growth of mycelium has recently been verified and extended by Javillier,<sup>12</sup> who has made comparative cultures with increasing doses of zinc salt. He grew *Sterigmatocystis* for four days at 34° C. in media with graded additions of zinc salts. As the graphic representation shows, he finds a continuous

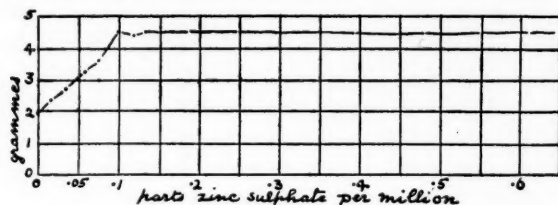


FIG. 4.

regular increase of the number of grams of final dry weight with doses up to 0.00001 per cent., and then no greater but an equal effect up to 100 times as large a dose.

This form of curve with uniform rise at first, abruptly changing to a level top, suggests, as I have pointed out elsewhere,<sup>13</sup> the cutting-off of the primary rising effect by a limiting factor. In this case presumably the limit set by some other sub-section of the metabolism has been attained.

#### ACCELERATION OF REACTION-VELOCITY BY TEMPERATURE.

We now turn to consider the fourth and last of the principles of chemical mechanics which we might expect to find manifested in metabolism.

It is a universal rule that rise of temperature quickens the rate at which a chemical reaction proceeds. Of course in some rare conditions, this may not be obvious, but be obscured by superposed secondary causes; but almost always this effect is very clearly marked.

Further, the nature of the acceleration is a peculiar

<sup>12</sup> *Comptes rendus de l'Acad. des Sciences*, December, 1907.

<sup>13</sup> Optima and Limiting Factors. *Annals of Botany*, Vol. XIX, April, 1905.

one. Rise of temperature affects nearly all physical and chemical properties, but none of these is so greatly affected by temperature as is the velocity of chemical reaction. For a rise of  $10^{\circ}$  C. the rate of a reaction is generally increased two or three fold, and this has been generalized into a rule by van't Hoff. As this increase is repeated for each successive rise of  $10^{\circ}$  C. either by the same factor or a somewhat smaller one, the acceleration of reaction-velocity by temperature is logarithmic in nature, and the curve representing it rises ever more and more steeply. Thus keeping within the vital range of temperature a reaction with a temperature factor of  $\times 2$  per  $10^{\circ}$  C. will go sixteen times as fast at  $40^{\circ}$  C., as at  $0^{\circ}$  C., while one with a factor of  $\times 3$  will go eighty-one times as fast.

This general law of the acceleration of reactions by temperature holds equally for reactions which are being accelerated by the presence of catalysts. As we regard the catalyst as merely providing for the particular reaction it catalyzes, a quick way round to the final stage by passing through the intermediate stage of forming a temporary addition-compound with the catalyst itself, so we should expect rise of temperature to accelerate similarly these substituted chemical reactions.

If this acceleration is a fundamental principle of chemical mechanics it is quite impossible to see how vital chemistry can fail to exhibit it also.

#### ACCELERATION OF VITAL PROCESSES BY TEMPERATURE.

At present we have but a small number of available data among plants to consider critically from this point of view. But all the serious data with which I am acquainted, which deal with vital processes that are to be considered as part of the protoplasmic catalytic congeries, do exhibit this acceleration of reaction-velocity by temperature as a primary effect.<sup>14</sup>

<sup>14</sup> A collection of twenty cases, mostly from animal physiology, by Kanitz (*Zeits. für Elektrochemie*, 1907, p. 707), exhibits coefficients ranging from 1.7 to 3.3.

Let us briefly consider these data. On the katabolic side of metabolism we have the respiratory production of  $\text{CO}_2$ , and opposed to it on the anabolic side the intake of carbon in assimilation.

As a measure of the rate of the metabolic processes constituting growth we have data upon the division of flagellates; and finally there is the obscure process of circulation of protoplasm.

The intensity of  $\text{CO}_2$  production is often held to be a measure of the general intensity of metabolism, but any relation between growth-rate and respiration has yet to be clearly established. Our science is not yet in the stage when quantitative work in relation to conditions is at all abundant; we are but just emerging from the stage that chemistry was in before the dawn of physical chemistry.

Taken by itself the  $\text{CO}_2$ -production of an ordinary green plant shows a very close relation with temperature. In the case of the cherry-laurel worked out by Miss Matthæi and myself the respiration of cut leaves rises by a factor of 2.1 for every  $10^\circ \text{C}$ . (See Fig. 5, Resp.) This has been investigated over the range of temperatures from  $16^\circ \text{C}$ . to  $45^\circ \text{C}$ . At this higher temperature the leaves can only survive ten hours in the dark, and their respiration is affected in quite a short time, but in the initial phases the  $\text{CO}_2$  output has the value of .0210 gr. per hour and unit weight of leaf, while at  $16.2^\circ \text{C}$ . the amount is only .0025 gr.  $\text{CO}_2$ . Thus the respiration increases over a range of tenfold with perfect regularity solely by increase of temperature. No reaction in a test-tube could show less autonomy. At temperatures above  $45^\circ \text{C}$ . the temperature still sooner proves fatal unless the leaf is illuminated so as to carry out a certain amount of photosynthesis and compensate for the loss of carbon in respiration. Thus, with rising temperature, there is at no time any sign of an optimum or of a decrease of the intensity of the *initial* stage of respiration.

Here, then, on the katabolic side of metabolism we have no grounds for assuming that "temperature-stimuli" are at work regulating the intensity of protoplasmic respira-

tion, but we find what I can only regard as a purely physical-chemical effect. The numbers obtained by Clausen<sup>15</sup> for the respiration of seedlings and buds at different temperatures indicate a temperature coefficient of about 2.5 for a rise of 10° C.

To this final process of katabolism there could be no greater contrast than the first step of anabolism, the assimilation of carbon by the protoplasm as a result of photosynthesis. We must therefore next inquire what is the relation of this process to temperature.

This question is not so simple, as leaves can not satisfactorily maintain the high rate of assimilation that high temperatures allow. The facts of the case were clearly worked out by Miss Matthæi,<sup>16</sup> the rate of assimilation by cherry-laurel leaves being measured from -6° C. to +42° C. Up to 37° C. the curve rose at first gently and then more and more steeply, but on calculating out the values it is found that the acceleration for successive rises of 10° C. becomes less and less. Between 9° C. and 19° C. the increase is 2.1 times, the highest coefficient measured, and exactly the same coefficient as for respiration in this plant, which in itself is a striking point, seeing how different the processes are. (See Fig. 5, Assimilation.)

The decrease of the coefficient with successive rises is a state of things which is quite general among non-vital reactions. A critical consideration of the matter leads one to the conclusion, however, that this failure to keep up the temperature acceleration is really due to secondary causes, as is also the appearance of an optimum at about 38° C. Some of these causes, have been discussed by me elsewhere,<sup>17</sup> and I hope to bring a new aspect of the matter before the section in a separate communication. The conclusion formerly come to was that probably in its initial stages assimilation at these very high tempera-

<sup>15</sup> *Landwirtschaftliche Jahrbücher*, Bd. XIX, 1890.

<sup>16</sup> *Phil. Trans. Roy. Soc., Ser. B*, Vol. CXC VII, 1904.

<sup>17</sup> Optima and Limiting Factors. *Annals of Botany*, Vol. XIX, April, 1905.

tures started at the full value indicated by a theoretically constant coefficient, but that the protoplasm was unable to keep up the velocity, and the rate declined. It must be borne in mind here that quite probably no chloroplast

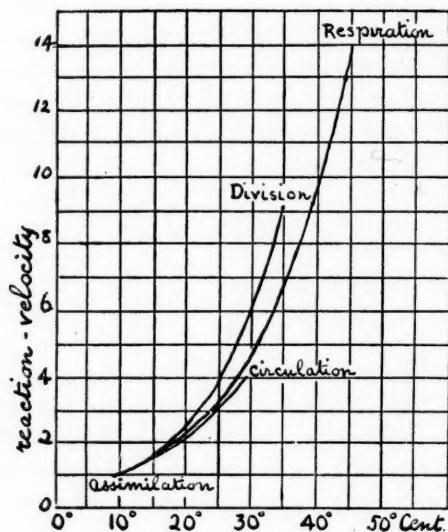


FIG. 5.

since the first appearance of green cells upon the earth had ever been called upon for anything like such a gastronomic effort as these cherry-laurel leaves in question. It is not to be wondered that their capacities speedily declined at such a banquet, and that the velocity-reaction of anabolic synthesis traces a falling curve in spite of the keeping up of all the factors concerned, to wit, temperature, illumination, and supply of  $\text{CO}_2$ . This decline is not permanent, but after a period of darkening the power of assimilation returns. Physical-chemical parallels can easily be found among cases where the accumulation of the products of a reaction delays the apparent velocity of the reaction, but this complicated case may be left for further research.

In relation to assimilation, then, we must say that

owing to secondary causes the case is not so clear over the whole range of temperature as that of respiration, but that at medium temperatures we have exactly the same relation between reaction-velocity and temperature.

We may consider now some data upon the combined net result of anabolic and katabolic processes. Such total effects are seen in their clearest form among unicellular saprophytic organisms for which we have a few data. Mlle. Maltaux and Professor Massart<sup>18</sup> have published a very interesting study of the rate of division of the colorless flagellate *Chilomonas paramecium* and of the agents which they say stimulate its cell-division, in particular alcohol and heat.

They observed under the microscope the time that the actual process of division into two took at different temperatures. From 29 minutes at 15° C. the time diminished to 12 minutes at 25° C., and further to 5 minutes at 35° C. The velocities of the procedure at the three temperatures 10° C. apart will therefore be in the ratio of 1 : 2.4 : 5.76, which gives a factor of 2.4 for each rise of 10° C. (See Fig. 5, Division.)

Now we are told by the investigators that at 35° C. *Chilomonas* is on the point of succumbing to the heat, so that the division rate increases right up to the death point, with no sign of an optimum effect. Below 14° C. no observations are recorded.

Here, then, we have throughout the whole range exactly the same primary temperature relation exhibited by the protoplasmic procedure that we should expect for a chemical reaction in a test-tube.

This division phase is only a part of the life-cycle of the flagellate, and between division it swims about anabolizing the food material of the medium and growing to its full size ready for the next division. One wishes at once to know what is the effect of the temperature upon the length of the life-cycle. Is the whole rate of metabolism quickened in the same way as the particular section con-

<sup>18</sup> Maltaux and Massart. *Recueil de l'Institut botanique Bruxelles*, Tome VI, 1906.

cerned with actual division? Of course a motile flagellate can not be followed and its life-cycle directly timed but the information was obtained by estimating carefully what percentage of individuals was in a state of actual division at each temperature. It was found that always 4 per cent. were dividing, whatever the temperature. This proves that the whole life-cycle is shortened in exactly the same proportion as the process of division at each temperature, and that it is just twenty-five times as long. Therefore the life-cycle is 125 mins. at 35° C. and 725 mins. at 15° C., so that here, again, we have the physical-chemical relation with a factor of 2.4 for each rise of 10° C.

In this paper of Maltaux and Massart these relations are not considered as the manifestations of physical-chemical principles, but are regarded as reactions to stimuli; and the paper contains a number of experiments upon the effect of sudden changes of temperature upon the occurrence of division. As far as one can make out from inspection of the scattered literature, it does seem established that sudden changes of temperature act as stimuli in the strict sense of the word. In many investigations one finds it stated that a quick change of temperature produced a certain reaction which a slow change of temperature failed to evoke. Usually all the phenomena are treated in terms of stimulation, and the absence of reaction with slow change of temperature is regarded as secondary. Were it not for the specific stimulatory effects of quick change, which are not difficult to comprehend as a phenomenon *sui generis*, I hardly think so general a tacit acquiescence would have been extended by botanists to the view that all enduring changes of velocity of metabolism brought about by lasting changes of temperature are stimulatory in nature.

No determination of the rate of development of bacteria through a very wide range of temperature seems to have been made. There are various incidental experiments which indicate values about 2 for the coefficient of increase of metabolism for a rise of 10° C.

I am not acquainted with any data for the growth rate of whole flowering plants at different temperatures: Of course the case of growth most usually measured in the laboratory, namely, where one part of a plant extends at the expense of the reserves stored in another part and there is a decrease, not an increase, of total dry weight, is not the type of growth we have to deal with. Even for simple elongation of a shoot at different temperatures we have but few data. Those of Koppen (1870) generally quoted are wildly irregular, and in many cases it is clear that the growth-extension of complex structures is a process which proceeds by spasms rather than smoothly.

The rate of movement of circulating protoplasm increases rapidly with temperature, but Velten's numbers do not give an obvious logarithmic curve. If we confine our attention to the values for 29° C. and 9° C. we do find, however, that the velocity increases about two-fold for each rise of 10° C. being 10 mm. at 9° C. and 40 mm. at 29° C.

Taken altogether these various data clearly support the hypothesis that temperature accelerates vital processes in the same way as it does non-vital chemical reactions, that is, logarithmically by an approximately constant factor for each rise of 10° C.; and, further, it accelerates them to the same extent; that is, that the factor in question has values clustering about 2-3.<sup>19</sup>

To make these similarities more significant I ought to point out that no other properties of matter are accelerated to anything like this extent by rise of temperature. Most reactions increase in velocity by no less than 10 per cent. per degree rise of temperature; a most marked effect, and yet there is no generally accepted explanation of this almost universal phenomenon. By the kinetic theory of gases each rise of a degree in temperature increases the movements of the gas-molecules, so that the

<sup>19</sup> It has been proposed to use the size of the temperature coefficient to settle whether a process like the conduction of an impulse along a nerve is a chemical or a physical process. See Lucas, Keith. *Journal of Physiology*, Vol. XXXVII, June, 1908, p. 112.

number of collisions between them is greater, but only about  $\frac{1}{4}$  per cent. greater. With rise in temperature, too, the viscosity of a solution diminishes, so that there is less resistance to internal changes; but this only to the extent of 2 per cent. per degree. The degree of ionization also increases, but only extremely little, so that no change of known physical properties will explain the phenomenon. Various hypotheses which need not detain us have been put forward.

Unexplained though it may be, yet the quantitative treatment of the subject is clear enough and, I think, as cogent in the living organism as in the test-tube. If so, we may consider ourselves now justified in separating off from the realm of stimulation yet a third class of causal connection, namely, that between temperature and general intensity of vital processes.

#### CONCLUSION.

In this attempt to assert the inevitableness of the action of physical-chemical principles in the cell, I have not ventured upon even the rudiments of mathematical form, which would be required for a more precise inquiry. Biochemistry is indeed becoming added to the ever-increasing number of branches of knowledge of which Lord Bacon wrote:

Many parts of nature can neither be invented with sufficient subtilty, nor demonstrated with sufficient perspicuity, nor accommodated unto use with sufficient dexterity, without the aid and intervening of the mathematics.

In this sketch which I have had the honor of outlining before you I have critically considered but few points. I have rather endeavored to distribute imperfect data in the perspective in which they appear from the point of view of one who seeks to simplify phenomena by extending the principles of chemical mechanics as far as possible into the domain of vital metabolism. Much critical quantitative work has yet to be done before the whole becomes an intelligible picture.

To me it seems impossible to avoid regarding the fun-

damental processes of anabolism, katabolism and growth as slow chemical reactions catalytically accelerated by protoplasm and inevitably accelerated by temperature. This soon follows if we once admit that the atoms and molecules concerned possess the same essential properties during their brief sojourn in the living nexus as they do before and after.

Perhaps the more real question is rather as to the importance and significance of this point of view. Protoplasmic activity might be something so much *per se*, and the other factors of the nature of stimuli might be superposed so thickly upon that substratum which should be dominated by simple principles of chemical mechanics that for practical purposes the operations of the latter would be so overlaid and masked as to be negligible. A survey of this field, however, seems to show that this is not so, and that the broad action of the law of mass and the acceleration of reaction-velocity by temperature are obviously responsible for wide ranges of phenomena.

Now the conception at the bottom of these principles is that of reaction-velocity, and the conclusion of the whole matter is that the physiologist must frankly take over from physical chemistry this fundamental conception.<sup>20</sup> Under definite conditions of supply of material and temperature there is a definite reaction-velocity for a given protoplasm, and the main factors that alter the rate of metabolism, viz., heat, nutrition and traces of impurities are exactly the factors which affect the velocity of reactions *in vitro*.

Working on this basis we no longer need the vague unquantitative terminology of stimulation for the most fundamental of the observed "responses" to external con-

<sup>20</sup>No general treatment of the physiology of plants has yet been attempted in terms of reaction-velocity. Czapek, however, in the introduction to his stupendous *Biochemie der Pflanzen*, Vol. I, 1905, does draw attention to the conception of "reaction-velocity" and refers to the standard literature on this subject and on catalysis, though direct application is not made to the plant. Cohen (*Physical Chemistry for Physicians and Biologists*, English edition, 1903) considers in detail some biological applications of the acceleration of reactions by temperature.

ditions. Three sets of phenomena we have observed which, though usually treated in the category of stimulation, draw a clearer interpretation from the conception of reaction-velocity. These were: (1) the relation of development to the absence or deficit of single essential food constituents; (2) the occasional striking effect of minute traces of added foreign substances upon the whole rate of growth and metabolism; and (3) the general doubling of the activity of vital processes by a rise of  $10^{\circ}$  C.

The next higher stratum of principles should be the complications introduced by limiting factors which interrupt the extent of the manifestations of these principles and by various correlations, as, for example, that by which the reaction-velocity of one catabolic process might withdraw the supply of material needed for full activity of another different process. To this sort of relation may be attributed that phenomenon so characteristic of the more complex vital processes and quite unknown in the inorganic world, namely, the optimum.

Finally, superposed upon all this comes the first category of phenomena that we are content still to regard as stimulatory. From the point of view of metabolism and reaction-velocity many of these appear very trivial, though their biological importance may be immense. Think how little the tropistic curvatures of stems and roots affect our quantitative survey; yet a little rearrangement of the distribution of growth on the two sides of an organ may make the difference between success and failure, between life and death.

From our present point of view vision does not extend to the misty conceptions of stimulation upon our horizon. We may therefore postpone speculation upon the mechanical principles governing them and await the time when by scientific operations we shall have reduced to law and order the intervening region, which we may entitle the chemical substratum of life. This done we may venture to pitch our laboratory a march nearer to the phenomena of protoplasmic irritability and make direct attack upon this dominating conception, the first formidable bulwark of vital territory.

## THE DESICCATION OF ROTIFERS

D. D. WHITNEY

COLD SPRING HARBOR, LONG ISLAND, N. Y.

THE general statement often found in text-books that "Adult rotifers can survive prolonged desiccation and resume active life when again placed in water," seems to have been made without sufficient warrant.

While working with the rotifer, *Asplancha brightwellii*, my attention was repeatedly called to the fact that when the water became sufficiently evaporated so as to expose only a portion of the body of the rotifer to the air it never recovered when placed again in a larger quantity of water and soon died. Doubt as to the truth of the general statement regarding desiccation naturally arose and in consequence a series of experiments were carried out to test the matter.

Forty-five species of rotifers that were collected in the various ponds and pools in the vicinity of Cold Spring Harbor, New York, were dried at room temperature, from a few hours to several days, during the months of July and August. They were dried without being exposed to direct sunlight in a hollow ground slide, upon filter paper, in sediment taken from the water in which the rotifers lived, and also in sediment mixed with sand. Masses of the water plants, *Lemna*, *Myriophyllum* and others among which many species lived were also dried. After the water seemed to have been completely evaporated fresh spring water was added and those animals that ever revived did so within ten to twenty minutes after the water was added. Drying the rotifers in masses of sediment and in sediment mixed with sand was found to lead to more recoveries.

In all experiments many species were dried in the same lot and in nearly all of them these were mixed with rotifers which were known to withstand drying. If none of

the animals revived when water was added it was assumed that the method of drying of the lot was imperfect but if, on the other hand, those animals that were known to be able to withstand drying revived, when water was added, the method of drying of the lot was deemed satisfactory. It may be possible, however, that the individuals of different species, since they vary greatly in size and form, require different methods for being successfully dried and again revived. But if revival after desiccation is of general occurrence for adult rotifers the various methods of drying used in the experiments ought to have given a fair percentage of positive results.

The individuals of some of the species were obtained in countless thousands, either in nature or in artificial cultures, others were less numerous and only a few thousand or a few hundred individuals were obtained. In a small number of species only a few individuals were found and used in the experiments.

Jennings<sup>1</sup> classifies the rotifers in five orders: (1) Bdelloida with two families; (2) Seisonacea with one family; (3) Rhizota with three families; (4) Ploima with eighteen families; and (5) Scirtopoda with one family.

In the experiments performed no individuals were used belonging to the order Seisonacea which contains all marine forms, nor were there used any individuals of the order Rhizota which contains all the fixed forms, Representatives were used from one family of the order Bdelloida, from fifteen families of the order Ploima, and from the one family of the order Scirtopoda. Thus the forty-five species used represented seventeen of the twenty-one families in the three orders just mentioned.

The following species were used in the experiments:

Order 1. Bdelloida.

Family 1. Philodinadæ.

Species. *Rotifer vulgaris*,<sup>2</sup> *R. macrurus*,<sup>2</sup> *Philodina roseola*,<sup>2</sup>  
*P. citrina*.<sup>2</sup>

Order 4. Ploima.

Suborder 1. Illoricata.

<sup>1</sup> AMER. NAT., Vol. XXXV, p. 725.

## Family 1. Microcodontidæ.

Species. *Microcodon clavus*.<sup>4</sup>

## Family 2. Asplanchnadæ.

Species. *Asplanchna brightwellii*.<sup>3</sup>

## Family 3. Synchætadæ.

Species. *Synchæta tremula*,<sup>5</sup> *Polyarthra platyptera*.<sup>2</sup>

## Family 4. Triarthradæ.

Species. *Triarthra longiseta*.<sup>3</sup>

## Family 5. Hydatinadæ.

Species. *Hydatina senta*.<sup>3</sup>

## Family 6. Notommatadæ.

Species. *Taphrocampa saundersia*,<sup>4</sup> *Notommata* ———,<sup>5</sup>*Copeus pachyurus*,<sup>5</sup> *Furcularia gracilis*,<sup>2</sup> *F.* ———<sup>4</sup>*Eosphora aurita*,<sup>3</sup> *Diglena* ———.<sup>5</sup>

## Suborder 2. Loricata.

## Family 1. Rattulidæ.

Species. *Mastigocerca mucosa*,<sup>2</sup> *M. bicornis*,<sup>2</sup> *M.* ———.<sup>3</sup>

## Family 2. Dinocharidæ.

Species. *Dinocharis tetractis*,<sup>4</sup> *Scaridium longicaudatum*,<sup>5</sup>*S. endactylotum*.<sup>5</sup>

## Family 3. Salpinadæ.

Species. *Salpina eustala*.<sup>2</sup>

## Family 4. Euchlanidæ.

Species. *Euchlanis dilatata*,<sup>5</sup> *E. triquetra*.<sup>4</sup>

## Family 5. Cathypnadæ.

Species. *Cathypna leontina*,<sup>4</sup> *Distyla gissensis*,<sup>2</sup> *D. stokesii*,<sup>4</sup> *Monostyla lunaris*,<sup>2</sup> *M. bulla*,<sup>2</sup> *M. quadridentata*.<sup>2</sup>

## Family 6. Coluridæ.

Species. *Colurus bicuspidatus*,<sup>5</sup> *Metopidia lepadella*,<sup>3</sup> *M. triptera*,<sup>2</sup> *M.* ———.

## Family 7. Pterodinadæ.

Species. *Pterodina patina*,<sup>4</sup> *P. reflexa*.<sup>4</sup>

## Family 8. Branchionidæ.

Species. *Branchionus bakeri*,<sup>5</sup> *B. urceolaris*,<sup>3</sup> *B. pala*,<sup>2</sup> *B. angularis*,<sup>3</sup> *Noteus quadricornis*.<sup>5</sup>

## Family 10. Pleosomadæ.

Species. *Pleosoma truncatum*<sup>2</sup> (?).

## Order 5. Scirtopoda.

## Family Pedalionadæ.

Species. *Pedalion mirum*.<sup>2</sup><sup>2</sup> Few thousand individuals used in the experiments.<sup>3</sup> Many thousand individuals used in the experiments.<sup>4</sup> Probably less than a hundred individuals used in the experiments.<sup>5</sup> Few hundred individuals used in the experiments.

This list is far from being complete but it represents so many families of the free swimming rotifers upon which the general statement in regard to desiccation is supposedly based that the results obtained ought to indicate whether the phenomenon of desiccation is widespread among the common forms.

*Philodina roseola* and *Philodina citrina* were the only forms of the forty-five experimented upon which could successfully withstand desiccation and resume normal activities when again placed in water. Some of them remained ten days in small masses of débris, 1-2 mm. in diameter, which were as thoroughly dried as possible in the laboratory atmosphere. Those that were dried in the sun never revived when again placed in water. This may have been due to a too complete desiccation or to the high temperature, which was usually about 45° C.

The cuticle in the Philodinadæ is less specialized in the structure than in any of the other families of the three orders, and as this structural character is of great importance in the present system of classification the family may be considered the lowest or most primitive of all the twenty-one families. It is interesting to note, however, that some of the species of another genus, *Rotifer*, of the same family, can not withstand complete desiccation. In several experiments in which the four species of *Philodina* and *Rotifer* were mixed together in the débris, sediment or water plants, all four species would revive if the material in which they were contained was not completely dried, but only the two species of *Philodina* revived when the drying was complete. Systematists separate the two genera by the position of the eyes but evidently there is a more fundamental difference than this which means life and death in times of drought.

The common misconception regarding desiccation may probably have arisen, in part, from the fact that when mud or sediment from ponds in which rotifers live is dried living rotifers appear after a few hours when water is added to the sediment. These living rotifers prob-

ably develop however from the "winter eggs"; thick shelled fertilized eggs, which in some cases are known to withstand prolonged desiccation.

During this summer some winter eggs of *Asplanchna brightwellii* and *Hydatina senta*, which had been laid in June, were kept in water taken from the culture<sup>6</sup> jars until August 3. Then they were taken out with a little sediment and allowed to dry. On August 5, the sediment was apparently thoroughly dried. On August 10 spring water was added and at the end of twenty-four hours several small *Asplanchna* were swimming about in the water. Later young *Hydatina* were found in the water. The eggs seem to vary much in the length of time required for them to hatch, some not hatching for three or four days after being placed in spring water while others hatch within twenty-four hours. This may be due to differences in the rate of rapidity in which water penetrates the egg membranes. In sections of the winter eggs of *Hydatina senta* it is very noticeable that the thickness of the outer egg membrane varies greatly in different eggs.

On August 4 ten to fifteen cubic centimeters of mud and sediment were collected in a finger-bowl from the pond in which *Asplanchna brightwellii*, *Branchionus urceolaris*, and *Pedalion mirum*, were living and allowed to dry in the sun. The next day the mud was thoroughly dried so it would readily crumple between one's fingers. In this condition it was kept until August 10 when the finger-bowl was filled with spring water. On the following day several individuals of each of the above three species were swimming about in the water.

When ponds and pools in which rotifers live are in the process of drying up the water becomes so foul by the decomposition of dead plants and animals that all the rotifers of some species die before the pool is completely dried. If, on the other hand, rotifers are kept in the laboratory in very clean water which is allowed to slowly

<sup>6</sup> *Jour. Exper. Zool.*, Vol. V, p. —.

evaporate they all die, presumably of starvation. It is also interesting to note that some pools do not become dry during the summer but the rotifer fauna changes completely several times during the season. A small pond in this vicinity was teeming with *Asplanchna brightwellii* and *Branchionus urceolaris* during the early part of July but by the middle of August not an individual of either species could be found in it. Individuals of *Pedalion* and *Polyarthra* were very numerous at this time but in the latter part of August not one could be found. The pond was now teeming with *Branchionus angularis*, *B. pala* and *Triarthra longiseta* but no individual of the first four species named above was present.

In a case like this desiccation could play no part in the preservation of the species and they could only be saved by winter eggs.

Some winter eggs of *Asplanchna brightwellii* which were laid in June in artificial cultures were buried July 3 in an ice house upon a cake of ice where the temperature was 1-2° C. On August 7 they were removed from the ice house to ordinary room temperature and the old culture water replaced by fresh spring water. At the end of forty hours several young *Asplanchna* were swimming about in the water.

Many other winter eggs which were laid at the same time as the above lot but which had remained in the laboratory at room temperature in a bottle containing water, taken from the culture jar in June were placed in fresh spring water. In many cases within an hour the thick outer egg membrane had cracked open and exposed about a fourth of the thin inner membrane which surrounded the embryo. The history of some of these eggs was followed and it was found that they produced normal young animals on the following day. The swelling and cracking open of the thick outer membrane is obviously due to the sudden great change of osmotic pressure which is

brought about by removing the eggs from a somewhat foul and concentrated culture to fresh spring water.

This process of causing winter eggs to develop in the summer is very likely the same that occurs in nature in the spring months. During the fall and winter the pools become free from abundant animal and plant forms and the accompanying products of decomposition by the frequent floodings by rains and the low temperature. In the spring the heavy rains flood the pools again and the osmotic pressure of the water is so much lower than it was in the previous summer that the eggs absorb water enough to rupture the thick outer membrane and stimulate the embryos to growth. As the temperature becomes favorable they develop and the life cycle is completed.

From the foregoing observations it seems probable that desiccation of the adult rotifers followed by revival is not of widespread occurrence in the group and is not the means resorted to by most species for tiding over unfavorable periods. Survival is due in most cases to the winter eggs which can withstand both desiccation and a low temperature.

ON THE HABITS AND THE POSE OF THE SAUROPODOUS DINOSAURS, ESPECIALLY OF DIPLODOCUS

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To most persons the habits of living animals are more interesting than is their anatomy. The same is probably even more true with respect to the extinct animals. However, when it comes to determining the habits of extinct animals, their aquatic or terrestrial habitat, their modes of progression, their bearing on their limbs, their food and their ways of procuring it, their modes of attack and defense against their enemies, their manner of reproduction, etc., we meet with many difficulties.

The Sauropoda, and especially the species of *Diplodocus*, offer a fine illustration of the difficulties mentioned. Were they aquatic, or terrestrial, or amphibious? Did they affect dry lands, or swamps, or rivers and lakes? Did they eat vegetable food or did they prey on other animals? Did they chew their food or did they bolt it? Did they bring forth living young or did they lay immense eggs? Did they make bold attacks on their enemies or were they timid and cowardly creatures? Did they walk only, or swim only, or did they employ both methods of transporting their huge bodies? If they walked, was it on all four legs or on the hinder ones only? If on all four, did they carry their bodies high above the ground, after the manner of the ox and the horse, or did they carry them low down, like the crocodiles, perhaps dragging their bellies on the ground?

To some of these questions more or less definite answers have been made and accepted; others remain unanswered. It is pretty well agreed that a part of their time was passed in the water; that they could swim

readily; that they walked mostly on all fours; that to some extent at least they went about on land; that their food was mainly, if not wholly, vegetable; and that they had imperfect or no means of chewing it.

We are assisted in understanding the habits of these creatures by a knowledge of the nature of their environment. And this we must determine from the character of the deposits in which their bones are discovered and from the kinds of animals and plants accompanying them. Investigation has shown that their remains occur in sandstones and clays which were certainly laid down in fresh waters having no great amount of motion. The accompanying animals are other dinosaurs, some herbivorous, others carnivorous; besides crocodiles, turtles, freshwater fishes and freshwater shells. Some of the plants that occur in the deposits certainly lived in fresh water.

Hatcher<sup>1</sup> has discussed at length the nature of the region in which the species of *Diplodocus* and their allies lived, as well as the habits of the *Sauropoda* in general; and the present writer agrees with him on most points. Hatcher believed that the *Atlantosaurus* beds were deposited, not in an immense freshwater lake, as held by some geologists, but over a comparatively low and level plane, which was occupied by perhaps small lakes connected by an interlacing system of river channels. The climate was warm and the region was overspread by luxuriant forests and broad savannas. The area thus occupied included large parts of the present states of Colorado, New Mexico, Utah, Montana, and the Dakotas. In his memoir on *Diplodocus*, Hatcher<sup>2</sup> compares the conditions prevailing in that region during the Upper Jurassic to those now found about the mouth of the Amazon and over some of the more elevated plains of western Brazil. In such regions the rivers, fed from distant elevated lands, must have been subject to frequent inundations.

<sup>1</sup> *Mem. Carnegie Mus.*, II, 1903, pp. 54-67.

<sup>2</sup> *Mem. Carnegie Mus.*, I, p. 60.

The beds of the streams were continually shifting, and there existed numerous abandoned channels that were filled with stagnant water. An animal that lived in such a region would be compelled to adapt itself to a more or less aquatic life, and this adaptation would be reflected to a greater or less extent in the structure of the animal. Marsh had concluded from the position of the external nares of *Diplodocus* that it was addicted in some measure to an aquatic existence. The feet too are of rather peculiar structure, the inner toes being strongly clawed, the outer toes greatly reduced; but the meaning of this is differently interpreted.

#### THE FOOD OF DIPLODOCUS

The particular sort of food eaten by the species of *Diplodocus* is unknown, but nobody doubts that it was vegetable. The teeth were pencil-like in form and they were entirely confined to the front of the jaws. By general consent, they could have been employed only for prehension of food, not at all for its mastication. Hatcher suggested that the teeth might have been useful in detaching from the bottoms and shores the tender and succulent aquatic and semi-aquatic plants that must have grown there in abundance. Osborn<sup>3</sup> says that "the food probably consisted of some very large and nutritious species of water plant. The anterior claws may have been used in uprooting such plants. . . . The plants may have been drawn down the throat in large quantities without mastication." In a restoration of *Diplodocus* by Mr. Charles W. Knight<sup>4</sup> the animal is represented as standing on its hind legs and preparing to bite off the terminal bud of a towering cycad. Holland<sup>5</sup> thinks that the teeth were better adapted for raking and tearing off from the rocks soft masses of clinging algæ than for securing any other forms of vegetable food now represented in the waters of the world.

<sup>3</sup> *Mem. Amer. Mus. Nat. Hist.*, I, p. 214.

<sup>4</sup> *Scientific American*, XCVI, 1907, p. 485.

<sup>5</sup> *Mem. Carnegie Mus.*, II, p. 240.

To the present writer the suggestion of Dr. Holland has in it more of probability than any of the others presented. If the food-plants sought by *Diplodocus* had been large and such as required uprooting by the great claws of the reptile the prehension and manipulation of the masses would have been liable to break the slender teeth and would certainly have produced on them perceptible wear. The upper teeth of the original of Marsh's figures on Plate XXV of the *Dinosaurs of North America*<sup>6</sup> show no wear, so far as the writer can determine. The mandibular teeth are not well exposed to view.

With respect to Osborn's theory, it is well to take into consideration also the probable ability of the reptile to digest great masses of undivided and unmasticated vegetation. Against the theory suggested by Knight's restoration it may be urged that the teeth, pointed or slightly chisel-shaped, are poorly adapted for cropping leaves and great buds; most of all, the teeth have spaces between them, like the teeth of a great comb, an arrangement not favorable to their functioning as cutting instruments. The teeth could hardly have been used for scraping algae from rocks, either, for that usage would have produced evident and rapid wear. It is more probable that the food consisted of floating algae and of plants that were loosely attached to the bottoms of stagnant bayous and ponds. Hatcher has reported<sup>7</sup> the finding of the seeds and the stems of a species of *Chara* near the Marsh quarry, where many Sauropoda have been found. This alga, it seems to the writer, would have been admirably adapted to the needs of *Diplodocus*. It could be easily gathered into the mouth as the reptile swam or crawled lazily about or rested itself and retracted and extended its long neck. The long and highly vaulted palate would have permitted a considerable mass to be collected, out of which, by pressure of the tongue, the superfluous water might have been squeezed between

<sup>6</sup> (Cat. No. 2672, U. S. Nat. Mus.)

<sup>7</sup> *Mem. Carnegie Mus.*, II, p. 63.

the spaced teeth. In addition to various algæ there were probably other floating plants.

#### THE POSTURE OF DIPLODOCUS

Marsh presented no restoration of *Diplodocus*, but he did furnish restorations of *Brontosaurus*; and he stated that he regarded it as representing the general form and proportions of the *Sauropoda*. In this figure *Brontosaurus* is shown as walking with the body high above the ground and with the limbs, especially the hinder ones, about as straight as they are in the elephant.

So far as the bearing of *Brontosaurus* and *Diplodocus* on their limbs is concerned, Marsh's example has been almost slavishly followed ever since. No one, so far as the writer knows, has ventured to defend in print a more crocodilian posture. Osborn<sup>8</sup> grants that there is room for wide differences of opinion as regards the habits and means of locomotion of these gigantic animals and states that some hold the opinion that on land at least these reptiles had rather the attitude of the alligator. The same writer says in *Nature*, vol. 73, 1906, p. 283, that Dr. Matthew and Mr. Gidley have maintained the latter view. However, the trend of opinion seems to have been in the opposite direction. Osborn<sup>9</sup> suggested that *Diplodocus* might lift its fore limbs from the ground and support itself on the hinder legs and the tail. This idea has found expression in Knight's restoration referred to above. Osborn's general notion of *Diplodocus* seems, however, to be that it was essentially an aquatic animal, long, light-limbed, and agile, and capable of swimming rapidly by means of its great tail, provided, as he thought, with a vertical fin; yet occasionally going about on land. Hatcher<sup>10</sup> opposed the view that *Diplodocus* was aquatic; and he showed that there is no evidence of the presence of a vertical fin. The compression of the

<sup>8</sup> *Science*, XXII, 1905, p. 376.

<sup>9</sup> *Mem. Amer. Mus. Nat. Hist.*, I, p. 213.

<sup>10</sup> *Mem. Carnegie Mus.*, II, 1903, p. 59.

centra where the fin is supposed to have been situated seems to have been slight, and the neural spines are not higher than elsewhere. The present writer finds neither in the feet nor in the tail any special arrangements for swimming. For navigation in its restricted waters no fin was needed. Almost any colubrid snake makes fair progress in the water, notwithstanding the absence both of a compressed tail and of a vertical fin.

Hatcher's final view does not, after all, appear to have been greatly different from that of Osborn. He held that *Diplodocus*, as well as most of the Sauropoda, were essentially terrestrial animals, but that they passed much, perhaps most, of their time in shallow water, where they could wade about and search for food. He believed that they were ambulatory, but quite capable of swimming. Hatcher's language does not necessarily imply that these animals walked about after the fashion of quadrupedal mammals, but his restorations show plainly that such was his conception.

This conception has prevailed in the plaster reproductions of the skeleton of *Diplodocus* which have been sent abroad by the Carnegie Museum and set up in London, Berlin and Paris; and in the small plaster restorations issued by the American Museum of Natural History. However, the limit of quadrupedal erectness, rigidity, rectangularity, and rectilinearity has quite been reached in the skeleton sent by the last mentioned institution to the Senckenberg Museum, at Frankfort-on-the-Main. In this case the poor beast is made to stand straight-legged and almost on the tips of its digits. On the other hand, the American Museum's skeleton of *Brontosaurus*, a much larger and heavier reptile and one sorely needing the mechanical advantage of straight legs, in case it had to bear its body free from the ground, has been presented to the modern world as having been decidedly bow-legged.

To the present writer it appears that the mammal-like pose attributed to the Sauropoda is one that is not required by their anatomy and one that is improbable.

The current conception is one that is easily accounted for. Before exact knowledge of these reptiles had been gained, it was known that the dinosaurs of the other groups, herbivorous and carnivorous, walked erect, after the manner of birds. It was indeed necessary, on account of the length of the fore limbs, to place the Sauropoda on all four feet; but analogy caused it to be supposed that the limbs were disposed, with reference to the vertical plane of the body, similarly to those of the bipedal dinosaurs. The conception of a creeping dinosaur was hardly to be entertained. The straight femora of these reptiles, having the head and the great trochanter moderately developed, lent probability to the idea.

If the straightness of the femora is relied on to support the correctness of the prevailing restorations of the Sauropoda we may call attention to the equally straight femora of sphenodon and of the lizards. Notwithstanding the great size of the carnivorous dinosaur *Allosaurus* and the fact that the whole weight of its body was commonly borne by the hinder limbs alone, its femora are considerably bent. The prominence and the height of the great trochanter of the Sauropoda do not appear to be such as to have prevented the femora from standing out at right angles with the body. Both the head of the femur and the acetabulum were doubtless invested with much cartilage, so that we can not now be wholly certain about their form and fitting. The same may be said regarding certain other articulations of the limbs. Hatcher<sup>11</sup> has spoken of the character of the articulations and he has expressed the opinion that the habitual support of the body in the air could not have failed to produce closely applied and well-finished articulations, and Osborn had previously expressed the same idea.<sup>12</sup> There is indeed a great difference between the articulations of the limbs of the Sauropoda and those of the Theropoda, such as *Allosaurus* and *Ceratosaurus*.

<sup>11</sup> *Mem. Carnegie Mus.*, I, p. 59.

<sup>12</sup> *Bull. Amer. Mus. Nat. Hist.*, X, p. 220.

Osborn<sup>13</sup> has found in the large preacetabular process an argument in favor of the ability of *Diplodocus* to elevate the anterior part of its body. However, *Trachodon*, which habitually walked on its hind legs has a very insignificant preacetabular process. The crocodiles have a strongly developed process in front of the acetabulum.

It appears to the writer that the structure of the feet of the Sauropoda indicates that the digits were directed somewhat outward, instead of directly forward, as they are placed in the restorations. The strongly developed inner digits would then have come more effectively into contact with the ground than the much reduced outer digits and would have been employed by the animal as a means of pushing itself along. In case the lower end of the radius is placed in front of the ulna, as represented by Hatcher<sup>14</sup> it appears probable that the foot would be directed more strongly outward than is shown in his restoration.<sup>15</sup>

The writer is not aware that any one has held that the Sauropoda could not, at least while resting, assume a crocodile-like posture, with the abdomen on the ground and the limbs extended outward on each side. If such a position is admitted as possible, the arguments derived from the anatomy in favor of an erect mode of walking are greatly weakened. If such a pose was not assumed, what was the pose? Did *Diplodocus* and *Brontosaurus* lie down on their sides, as an ox or a horse does when sleeping? Or did they lie prone, with the limbs drawn up under them, as a dog sometimes does? These positions appear to be improbable. It is worth considering too what disposition *Diplodocus* made of its elephantine legs while it was swimming with the agility that has been imputed to it.

The weight of *Diplodocus* and of *Brontosaurus* furnishes a strong argument against their having had a

<sup>13</sup> *Mem. Amer. Mus. Nat. Hist.*, I, p. 210.

<sup>14</sup> *Mem. Carnegie Mus.*, II, p. 73, Fig. 1.

<sup>15</sup> *Op. cit.*, Pl. VI.

mammal-like carriage. There will be little dissent from the view that these animals inhabited a country in which marshy lands abounded and that they passed the most of their time in the vicinity of bodies of water. As to weight, Marsh estimated that that of *Brontosaurus* was more than twenty tons. Each footprint was thought to be about a square yard in extent. The pressure was therefore about 1,100 pounds on each square foot of the ground. What progress could such enormous animals have made through morasses and along mud-depositing rivers, in case they carried themselves as they are represented in the restorations? Without doubt, they would soon have become inextricably mired and would have perished miserably.

Osborn<sup>16</sup> has suggested that *Camarasaurus*, another sauropod was accustomed to wading about in rivers where the bottoms were sandy and firm. The habits of *Diplodocus* could have differed little from those of *Camarasaurus*. It is difficult to understand why an animal whose immediate ancestors must have walked about in a crocodile-like manner, an animal that was stupid and probably slow of movement, an animal which could by means of its long neck reach up from the bottom many feet to the surface and from the surface many feet to the bottom—why such a reptile should need to develop the ability to walk along river bottoms like a mammal. Furthermore, it seems somewhat overgenerous to impute to a reptile so many and so diverse activities as swimming with great facility, walking on river bottoms and on the land with mammal-like gait, and on occasion erecting itself on its hinder legs after the manner of a bird, in order to crop the foliage from the tops of high trees, when this reptile was sixty feet long, weighed many tons, had a brain little larger than one's two thumbs placed side by side, and was provided with a feeble dental apparatus with which to gather food wherewith to support its huge body, and that food of a sort that yielded little energy in proportion to its bulk.

<sup>16</sup> *Bull. Amer. Mus. Nat. Hist.*, X, p. 220.

The writer's conception of *Diplodocus* is that it was eminently amphibious, that it could swim with considerable ease, and that it could creep about on land, with perhaps laborious effort. When feeding it must have swam or crept lazily about, gathering in floating plants and such as were attached loosely to the bottom. If any plants that were relished grew at some depth they could be reached by the long neck; or, if there was foliage twenty feet above the water it could be as easily gathered in. That a *Diplodocus* ever stood on its hind legs is hardly more probable than that crocodiles may perform the same feat.

The large size of *Diplodocus* does not preclude the possibility that it could creep about on the land. *Crocodylus robustus*, of Madagascar, is said to attain a length of 10 meters, and yet it doubtless is able to walk as other crocodiles walk. The limb bones of *Diplodocus* and of *Brontosaurus* are proportionally as large as those of crocodiles.

It seems to the writer that our museums which are engaged in making mounts and restorations of the great Sauropoda have missed an opportunity to construct some striking presentations of these reptiles that would be truer to nature. The body placed in a crocodile-like attitude would be little, if any, less, imposing than when erect; while the long neck, as flexible as that of an ostrich, might be placed in a variety of graceful positions.

## SHORTER ARTICLES AND CORRESPONDENCE

### JUVENILE SUBSTITUTES FOR SMOKING TOBACCO

Nearly every boy has the desire to smoke and while many perhaps begin with tobacco itself, many more probably experiment with other substances of vegetable origin which burn well and yield readily the desired smoke so that the appearances, at least, of the act of smoking are produced. The knowledge of such substitutes in a particular locality is usually extensive and widespread, being the subject of serious conference and debate among the youthful inhabitants. Very little, if any, of this tradition is recorded, and it seems perhaps a matter of some botanical interest that it should be. In some ways, the practise of boys in thus providing a substitute bears a singular resemblance to that of the less civilized peoples or communities more or less isolated from tobacco-producing centers.

My own juvenile knowledge was obtained in eastern Connecticut between thirty and forty years ago. In those days there were still many umbrellas with rattan (*Calamus rotang?*) ribs. Short pieces of these, being porous, on being set afire at one end, a matter of some difficulty, allowed the smoke to be drawn through in sufficient quantities to be blown out through the mouth, but the smoke was hot and biting and the rattan was kept alight with difficulty. Later, I learned the virtues of the more generally used substitutes, hay-seed, sweet-fern and mullein. The hay-seed was usually procured from the floors of the hay barns and consisted of the more or less ripened florets of timothy (*Phleum pratense*) and redtop (*Agrostis* sp.) It was usually more or less carefully sifted and smoked in a clay pipe or packed in paper shells to imitate cigarettes. This was before the days of the universal use of hand-rolled cigarettes and no such papers were available, so we used a fairly stiff white paper, rolled it about a cylindrical piece of wood of desired length and diameter, fastening the free edge by means of home-made starch paste. When these were dry, they were carefully stuffed with the hay-seed and the ends carefully, if not skilfully, folded in. Very commonly, however, the ends came undone during the smoking and the fine hay-seed made a disagreeable mouthful. A more

popular filling consisted of the leaves of the sweet-fern (*Myrica asplenifolia*). The leaves were selected when green and fragrant, carefully dried in the sun or in the oven, until brittle, then thoroughly pulverized by rubbing between the hands, and finally sifted through a coarse sieve. This was then packed tight in cigarette shells, and sweet-fern cigarettes required some skill. The making of high-grade cigarettes of this kind was one of my specialties, and one summer I drove a thriving trade in them, disposing of a considerable number at the remunerative price of ten for one cent. The lower leaves of the common mullein (*Verbascum Thapsus*) were gathered chiefly as they were found dried on the plant, roughly pulverized and smoked in a clay pipe. They were supposed to closely resemble real tobacco and were the preparatory stage to genuine smoking. Often some small boy was inveigled into smoking fine-cut tobacco of the "Durham" or "Lone Jack" type under the impression that he was simply indulging in a pipe of mullein. The resulting sickness, as a rule, undeceived him and he realized too late that he had been made the victim of a joke more practical than pleasant.

For the long-cut tobacco, we found a fair substitute, at least in appearance, in the brown and dried ends of corn silk, but it was never so very popular with us. I have found on questioning, that these same substitutes were known to the generation preceeding mine and that they are equally well known to the generations coming on to fill our places. I have also learned of other substitutes not known to us as well as a widespread knowledge of some of those mentioned.

I find that there is a widespread use of tea and ground coffee for pipe smoking, and some use even of ground cinnamon. The older youth often take to cubebs, following the officinal use of the same. A use seems also to be made of the porous internodes of the grape-vine, as we used rattan, and even of tightly rolled tubes of cinnamon stick. I have also been told that some boys roll paper about the sticks of "punk" used to touch off fire crackers on the Fourth of July, and light and smoke them.

Inquiring of the boys in California, I find that they use corn silk and various leaves for pipe smoking. The leaves of maple, grape, fig, rose and willow are commonly employed. Perhaps the most popular of all are the leaves of the worm-wood (*Artemisia heterophylla*) which is common on most hillsides and gives a pleasing aromatic smoke. In many places, the old fallen leaves

of the blue gum (*Eucalyptus globulus*) is a favorite. The leaves of yerba santa (*Eriodictyon californicum*) is smoked to cure colds and also by the boys for the pure joy of smoking. The leaves of the California bay (*Umbellularia californica*) are often used in the same ways. I am informed by Dr. H. M. Hall that the composite *Atrichoseris platyphylla* is called "Tobacco weed" by the boys of Palo Verde, in the Colorado Desert of California and is in decided favor with them for smoking. This plant is decidedly rare to the botanist, but after heavy rains it becomes plentiful in sandy places and its broad basal leaves are well adapted to being rolled into "cigars."

Dr. G. H. Shull informs me that the leaves of the American pennyroyal (*Hedeoma pulegioides*) is smoked by the boys in some parts of Ohio.

The wild species of *Nicotiana* have furnished and still do furnish the smoking materials of certain aboriginal peoples from the neighborhood of Oregon south to Chile, but there is no record of their having been used by juveniles of the white races. I learn, however, from Professor R. H. Forbes, of the University of Arizona, that the "wild tobacco" of the neighborhood of Tucson, which, however, is *Nicotiana glauca*, the tree tobacco, is smoked by boys and without injurious effect.

The above facts are probably but a few of those on this subject which may be gathered and I trust that others may take sufficient interest to add to the list.

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## NOTES AND LITERATURE

### HEREDITY

**Recent Studies in Human Heredity.**—Must the fallacy always persist that all ancient and powerful families are necessarily degenerate? As long ago as 1881, Paul Jacoby wrote a book<sup>1</sup> to prove that the assumption of rank and power has always been followed by mental and physical deteriorations ending in sterility and the extinction of the race. By collecting together all evidence supporting his preconceived theory, by tracing only the well-known families in which pathological conditions were hereditary, by failing to treat of dozens of others whose records would not have supported his thesis, by saying everything he possibly could that was bad about every one (following always the hostile historians), by ignoring everywhere the normal and virtuous members, he was able to present what was to the uninformed an apparently overwhelming array of proof. In regard to the injustice of this one-sided picture I have already had something to say in "Mental and Moral Heredity in Royalty,"<sup>2</sup> first published some six years ago.

A further study based upon Jacoby's unsound foundations has recently come to my notice,<sup>3</sup> and although a well-made book containing an interesting series of 278 portrait illustrations, is necessarily quite as misleading as the older structure on which it rests. The main idea of Dr. Galippe is to show that the great swollen protruding underlip which descended among the Hapsburgs of Austria, Spain and allied houses, and also the protruding underjaw (*prognathisme inférieur*), are stigmata of degeneracy, and to demonstrate this he places beside his portraits, quotations from the writings of Jacoby.

Galippe uses no statistical methods, not even arithmetical counting, and appears to be totally ignorant of English biometric writings. His general conclusions about the causes of degeneracy (aristocratic environment, etc.) are quite as mis-

<sup>1</sup> *Études sur la sélection chez l'homme*. Paris, 1881, 2d ed., 1904.

<sup>2</sup> *Popular Science Monthly*, August, 1902–April, 1903. Also extended in book form, New York, Holt, 1906.

<sup>3</sup> V. Galippe. *L'hérédité des stigmates de dégénérescence et les familles souveraines*. Paris, 1905.

leading and unfounded as those of Jacoby, and I fear he could not even prove that the anatomical peculiarities are really stigmata of degeneration at all.

If abnormal mouths, noses and ears are to be proved the stigmata of degenerate or criminal types it is necessary to prove by biometrical methods, a correlation between the bodily anomalies on one hand, and the existence of psychic defect on the other. Galippe does not attempt to show such a correlation.

I have taken all the cases available, and divided Galippe's portraits into three classes, those in which the "lip" is "marked," those in which it is "slight" and those in which it is "absent." I have tried correlating these 205 cases with the mental and moral grades which I had previously obtained for these individuals; but I find that any correlation must be slight and difficult to prove without much larger data. For instance, of the distinctly inferior individuals 25 show the "lip" in a "marked" degree, against 20 in whom it is "absent"; while of the notably superior persons 22 have the "marked lip" against 21 in whom it is "absent." It may be similar to the slight correlation that is now thought to probably exist between genius and insanity. But this is not like saying that genius is insanity.

Many of Galippe's portraits labeled "*Prognathisme inférieur*" strike the reader as showing nothing peculiar in any way, others nothing more than a heavy underjaw, a common characteristic of the old royal personages, which so far from being a sign of degeneracy may as likely be associated with their general strength of character and determination of will.

But the most misleading side of Galippe's work, in which he also follows Jacoby, is his constant repetition of the word sterility and his frequent statements that noble and illustrious families thus find their natural end. The chief cause of this common mistake has arisen from following down, from ancient times to the more recent, the various dynasties in the male lines of primogeniture. In an appendix to Galton's "Natural Inheritance," 1889, this question is discussed, and it is there shown that *all* male lines, including the surnames of commoners, tend to diminish merely from the law of chance. This is because whenever all girls are born in any branch the name is lost absolutely, and can never be recovered. If the daughters marry and have children, the germ plasm is still transmitted, though

the name is no longer the same. The old dynasties, Plantagenet, Stuart, Romanoff, Vasa, etc., have become extinct in one sense, although not in another. If certain royal families have gone, what is to be said with regard to the following facts.

The male lines of all the present reigning families of Europe are carefully traced in the *opposite* direction, that is back to their earliest noble ancestors, in a most carefully compiled book by Dr. Kamil von Behr.<sup>4</sup>

With the exception of the present reigning family of Sweden, all have been princes, counts or dukes far into the remote past. These show from 20 to 33 generations of noble blood, in the direct male lines. The following is a list of the present royal families with the earliest authentic dates of their nobility. Anhalt 1059 A. D., Austria (Lorraine) 940 A. D., Baden 962 A. D., Bavaria 829 A. D., Belgium 1009 A. D., Denmark 1088 A. D., Great Britain 1009 A. D., Greece 1088 A. D., Hesse-Cassel 846 A. D., Hesse-Darmstadt 846 A. D., Italy (Savoy) 959 A. D., Liechtenstein 1133 A. D., Mecklenburg-Schwerin 960 A. D., Mecklenburg-Strelitz 960 A. D., Netherlands 992 A. D., Norway 1088 A. D., Portugal 1009 A. D., Prussia 1061 A. D., Reuss 1122 A. D., Rumania 1009 A. D., Russia 1088 A. D., Saxe-Coburg-Gotha 1009 A. D., Saxony 1009 A. D., Schaumburg-Lippe 1121 A. D., Schwarzburg 1114 A. D., Spain 861 A. D., Sweden 1810 A. D., Waldeck 940 A. D., Württemberg 1110 A. D. When one considers that they married practically always within their own ranks, one can easily see that the present reigning families are descended from thousands upon thousands of counts, dukes, princes, kings and emperors. That all this blue blood has not produced sterility is easily seen by a glance at the "Almanach de Gotha" or any of the books containing lists of the many children who have recently been born to royal families.

It is my own belief that much of the causation underlying historical records may be elucidated by the statistical method, if all cases for or against a certain theory be impartially recorded, and then even a simple arithmetical count be taken. The higher statistical methods (biometrical) may be useful for further refinement, but even the most simple rules of arithmetic would prevent one going quite as far astray from the truth as Jacoby and Galippe have done in their one-sided and utterly unjust arraignment of royal families. It is like picturing all million-

<sup>4</sup>Genealogie der in Europa regierenden Fürstenhäuser. 2d ed., Leipzig, 1870.

aires corrupt and dishonorable. Truly these slanderers of royalty, because they have a certain scientific affiliation, are all the more to be dreaded; furthermore, they cast discredit on the whole hope of any elucidation of history along biological lines.

In contrast to books of this sort, one gladly takes up several recent memoirs emanating from University College, London. In the first of the publications of the new Eugenics Laboratory, E. Schuster and Miss Elderton,<sup>5</sup> to obtain data bearing on the inheritance of ability, have made a statistical study of Oxford class lists and of the schools of Harrow and Charterhouse. By analyzing the academic standing of different members of the same family, they show that the resemblance between father and son is represented approximately by the coefficient  $r = .30$ , in all their tables. The various coefficients for fraternal resemblance, range around  $r = .40$ . They are perfectly in accordance with the theoretical expectancy propounded by Galton for his law of ancestral heredity. They are also in accordance with the correlations found in "Heredity and Royalty."

Other coefficients found by Pearson and his students for various physical and psychical measurements are higher than these, ranging around .40 to .50 for parental and .50 to .60 for fraternal correlation. In an appendix to this memoir of Schuster and Elderton, Pearson takes up the question of the size of the coefficients and shows that the class lists of Oxford, Harrow and Charterhouse represent probably a selected group, in point of ability, in which case their variability would be reduced and also the correlation coefficients. After making for this a reasonable, though rough, correction he concludes that the coefficients of Schuster and Elderton are in close accord with those heretofore found by this same school of investigators.

David Heron<sup>6</sup> from the same laboratory contributes a first study of the inheritance of the insane diathesis. It is indeed a "First Study" in more senses than one, for not only is it the first work on this question from the Eugenics Laboratory, but it is not too much to say that it is the first attempt to treat the whole subject in an exact and satisfactory manner from the

<sup>5</sup> *Eugenics Laboratory Memoirs*. I, The Inheritance of Ability. By Edgar Schuster, M.A., and Ethel M. Elderton. London, Dulau and Co., Soho Square, W., 1907.

<sup>6</sup> *Eugenics Laboratory Memoirs*. II, A First Study of the Statistics of Insanity and the Inheritance of the Insane Diathesis. By David Heron, M.A., London, Dulau and Co., Soho Square, W., 1907.

statistical standpoint. Heron, on this point, makes the following just and timely complaint.

A careful examination of the annual Reports of the Asylums of Great Britain and Ireland has led to the conviction that no data at present published would enable the statistician to reach any quantitative results as to the inheritance of any single form of brain disease. Even medical treatises as a rule go no further than stating the percentage of cases in which insanity or some other want of mental balance has been recorded in the family history. As long as we do not know the total number in each class of relatives of the insane person and the exact brain defect from which they have suffered; as long as we do not know the total number of relatives of a random sample of the sane population and the exact forms of neurosis or brain disease from which they too have suffered, any attempt at a full treatment of the "inheritance of insanity" is from the statistical standpoint idle. What advantage can possibly arise from telling us that an insane person has so many alcoholic uncles if we do not know either the total number of his parents brothers and sisters, or the percentage of alcoholic members in the same grade of relationship of a sane individual of the same social class? . . . The solution of this difficulty, and the present writer believes of many other difficulties in the statistics of insanity, is to establish a General Register of the Insane for preservation in the office of the Lunacy Commissioners.

Heron's own work is based upon an analysis of 331 family trees provided by Dr. A. R. Urquhart, physician superintendent of the James Murray's Royal Asylum, Perth, Scotland. The coefficient of parental inheritance is found to be about  $r = .50$  and fraternal resemblance  $r = .45 - .55$ . These are in close accord with other physical and mental measurements. The author is obliged to make several assumptions in regard to the general population in order to complete his calculations, so that his figures must be regarded as only a first approximation. The work is certainly in the right direction and it is to be hoped that all alienists will carefully read this valuable memoir.

Miss Elderton and Pearson<sup>1</sup> have published a measure of the resemblance of first cousins, especially in such characteristics as general health, intelligence, success, temper, temperament (reserved or expressive, sympathetic or callous, excitable or calm). Their correlation coefficients are not very uniform, but they show clearly enough a high degree of cousin resemblance,  $r$

<sup>1</sup> Eugenics Laboratory Memoirs. IV, On the Measure of the Resemblance of First Cousins. By Ethel M. Elderton, assisted by Karl Pearson London, Dulau and Co., Soho Square, W., 1907.

ranging around .27. The results are taken from Pearson's "Family Records" and there is something in the method which would seem to artificially increase the apparent resemblance. Different people have been asked to give their opinions about cousins whom they may happen to know. Some judges would naturally be more generous than others in their estimates. It is easy to see that, by cynicism on the one hand, and optimism on the other, many cousins would be taken in pairs out of the medium groups, where they very likely belong, and where they would lower the correlation coefficient, and placed in pairs either above or below the mean, where they would improperly raise the coefficients. Actual bodily measurements would not be susceptible of error from this source and these physical measurements they have attempted to obtain. So far, the latter records are insufficient for full publication, but as far as they go they show roughly a very high value for the coefficient  $r$ .

The authors "conclude accordingly, from the present results, that for the purposes of eugenics, cousins must be classed as equally important with uncles and aunts, and that they may eventually turn out to be as important as grandparents." One suggestion is that any scientific marriage enactments would equally allow or equally forbid marriage between first cousins, as between grandparents and grandchild, uncle and niece, or aunt and nephew.

One of their conclusions regarding alternate inheritance confirms my own general contention of alternate inheritance in mental and moral traits, a fact on which I laid so much stress in tracing the pedigree of all the royal families. They state that "a determinantal theory of heredity, emphasizing alternate inheritance, must take precedence of any theory of simple blending for the bulk of the characters here dealt with."

The next two memoirs to which I shall make reference,<sup>8</sup> are especially important and timely, owing to the wide-spread prevalence of the idea that tuberculosis is an infectious disease and not especially hereditary. I have even seen it printed in large

<sup>8</sup> Drapers' Company Research Memoirs, Studies in National Deterioration. II, A First Study of the Statistics of Pulmonary Tuberculosis. By Karl Pearson, F.R.S. Dulau and Co., London, 1907. Drapers' Company Research Memoirs. III, A Second Study of the Statistics of Pulmonary Tuberculosis: Marital Infection. By the late Ernest G. Pope. Adirondack Cottage Sanitarium, Saranac Lake, N. Y. Edited and revised by Karl Pearson, F.R.S., with an appendix on assortative mating from data reduced by Ethel M. Elderton. Dulau and Co., London, 1908.

type in publications emanating from public health leagues that "Tuberculosis Is Not Hereditary." I do not know on what scientific basis such a dogma rests.

Professor Pearson has found cogent proof in the first of these studies that the phthisical diathesis is just as hereditary as any human characteristic we know about. It would take too much space to completely review this paper. In a few words it may be enough to say that he does not jump at the conclusion that correlation coefficients necessarily show heredity. The question of infection through members of the same family living in close contact is discussed at length; but the analysis reveals no evidence that direct infection is in any way important, as compared to the heritable diathesis.

For instance, in his second paper on this same subject he finds that if a husband is tubercular, then there is a probability that the wife will also be found tuberculous, and *vice versa*, but this correlation is not nearly so high as that between brothers and brothers, sisters and sisters, and brothers and sisters. Yet opportunities for direct infection in the case of husband and wife are of course vastly greater than among brothers and brothers, etc., who by the time of the average age of onset of the disease (twenty to thirty years) have already ceased to live in the same households.

The question of assortative mating comes in to explain a certain amount of this observed correlation between husband and wife. Assortative mating is a convenient name for the tendency of like to mate with like, aside from any question as to what causes may bring about the similarity in question. It is a popular belief that tall men marry short women, and blonds are attracted by brunettes, but the truth of the matter seems to be quite the reverse. In nine series of physical characteristics the correlations of resemblance between husband and wife have been found to range between  $r=.20$  and  $r=.28$ . For physical characteristics nine series show a range between  $r=.11$  and  $r=.48$ , with an average of  $r=.24$ .<sup>o</sup> The correlation coefficient for insanity between husband and wife is  $r=.30$ .

"Unless, therefore, any characteristics show a relationship between husband and wife markedly greater than .20 to .25 it would be very

<sup>o</sup>"Second Study of the Statistics of Pulmonary Tuberculosis," cited above, p. 22.

difficult to assert that this resemblance is due to other causes than those assortative processes which have just been shown to produce quite a sensible degree of resemblance in husband and wife."

Pearson is "prepared to accept with some reservation a sensible but probably not very large infective action from the available statistics of pulmonary tuberculosis." The question of assortative mating is an important one, and a knowledge of the amount to be allowed under various circumstances seems to me to be a necessary adjunct for recorrecting all the correlation coefficients of heredity which have so far been obtained by the London workers. Their coefficients agree fairly well, but they are all distinctly higher than the theoretical—fraternal are about .50 to .60 instead of the theoretical .40; paternal .40 to .50, the theoretical being .30; and so with the most remote relationships, especially the first cousin resemblances.

It is evident that if assortative mating be in general the strong force that Pearson has shown it to be, then it must in most investigations raise the correlation coefficients for heredity. To make this clear—tall fathers have on the average tall sons, though their average height is less than that of the fathers, due to the principle of regression, but now if it happens that all the tall fathers have tall wives, then the sons will get an added height from the influence of the tall mothers and will seem to resemble their fathers more than they do from the real paternal influence alone.

Among royal families assortative mating is a disturbing factor is at a minimum, for here the marriages are so often arranged by others than the parties most concerned, or are the result of some important state policy, that the question of individual selection is nearly, though I believe not quite, eliminated. This may be the reason why the coefficients for heredity found in the study of royalty are so much nearer the theoretical.

It may be well, in closing, to say a word about the general question of correlation coefficients as affording a proof of the influence of pure heredity. It may be asked—do the coefficients really prove anything more than a general resemblance between relatives? May this not be due to heredity in some cases and to environment in others, or a combination of both, in most cases? Personally I do not feel that the coefficients alone afford all the desired proof. Analysis of the material, separating the cases into classes in which environment has had greater or less time

to act,<sup>10</sup> or into classes which are known to have lived in different environments, or comparing contrasted children within the same family, with contrasts in the ancestry of these (alternate inheritance) or other schemes which seek to find measurable influence of the environment factor, are, some or all, necessary for any final proof.

What the correlation coefficients *do* show is this, that if heredity be the great preponderating force, creating individual differences between man and man, the coefficients that have been found are in substantial agreement with what they should be.

Further refinement is wanted, especially as to the effect of assortative mating, and the shape of the curve of distribution for psychic characters, when selected classes are taken.

Mendel's laws, so important to the horticulturists, and to the breeder of superficial traits in fancy strains of domesticated animals, has not been shown to have any bearing on human heredity, at least as concerns important characteristics.<sup>11</sup> The general rough principle of alternate inheritance in human heredity, leads, however, to the hope that a further study of this question may bring out certain "unit characters," more or less marked, so that here in the end there may be harmony between the two unfriendly schools, the Mendelian and the Biometrical.

F. A. WOODS.

#### ORNITHOLOGY

**Riddle on the Cause of the Production of "Down" and other Down-like Structures in the Plumages of Birds.**<sup>1</sup>—A connection is here traced between the rate of growth and the character of the

<sup>10</sup> This method is employed by E. L. Thorndike in his excellent study of the "Measurement of Twins." *Arch. of Philos., Psychol. and Scientific Methods*, No. 1, New York, 1905. Also in some of the University College, London memoirs.

<sup>11</sup> It has been claimed to govern the inheritance of certain rare anomalies, albinism, abnormal hands, etc., also eye color (C. B. and G. C. Davenport, *Science*, Vol. XXVI, p. 589) and facial peculiarities of Red Indians when crossed with the Scotch (G. P. Mudge, *Nature*, November 7, 1907).

<sup>1</sup> Riddle, Oscar. The Cause of the Production of "Down" and other Down-like Structures in the Plumages of Birds. *Biological Bulletin*, Vol. XIV., No. 3, February, 1908, pp. 163-176.

structure in feathers. In a former paper<sup>2</sup> the same author showed that a feather is made up of a series of faint "fundamental bars," due to the manner of deposition of the feather substance. These bars are somewhat analogous to the annual rings of growth in the trunk of a deciduous tree, the tree rings showing the amount of annual increase in the tree trunk, while the bars mark the daily growth in the production of the feather. The demarkation of the fundamental bars is due to the period of reduced blood-pressure during the early morning hours (1-6 A.M.) of each day during the growth of the feather, and the defective transverse lines to malnutrition, or to reduced nutrition. As shown by Jones,<sup>3</sup> the nestling down or neossoptile is not a distinct and complete feather growth, but merely an apical segment of the first definitive feather, the first down being "the plumulaceous tip of the first definitive feather." The constriction between the two parts Riddle considers to be another variety of this same defect, due to insufficient nutrition. At the time of the hatching of the egg the down portion of the down feather is completed, and the shaft portion immediately succeeds, at a time when the whole source of food-supply is changed, and assimilation impaired by the intervention of a new source of alimentation. While this is obvious, experiments have been conducted to show the effects of underfeeding at the critical stage in the bird's life, and it has been found that a bird in the downy condition can thus be made to wear its downy plumage for months after it should have given place to the definitive feathers. "The 'quill' region is a part of the feather which 'normally' *almost* refuses to grow; by reducing the food-supply during and after its formation further growth may be absolutely inhibited or stopped."

From the experiments here related, the author concludes that the down portion of feathers is due to poor nutritive conditions, and that "The formation of the quill is probably the direct result of a progressive diminution of an already lessened food-supply."

Apparently all this bears upon the "how" rather than the "why" of feather production and feather structure, and is not to be given a too-sweeping application. In other words, that in the development of a pennaceous feather, the formation of its different parts—the pennaceous, the downy, and the quill por-

<sup>2</sup>A Study of Fundamental Bars in Feathers. *Biol. Bull.*, Vol. XII, February, 1907, pp. 165-174. Noticed in *The Auk*, January, 1908, p. 98.

tions—is not to be ascribed to the varying conditions of nutrition of the individual during the growth of a particular feather. While we would accept the hypothesis that varying blood-pressure during the twenty-four hours may give rise to the phenomena of “fundamental bars” and “defective lines,” that defective areas may result from malnutrition, and that under-feeding may retard feather development, we can hardly conceive that we have here a full explanation of the differentiation of a feather into pennaceous, downy, and quill portions, or that the widely differing plumage structure shown by owls, pigeons and hummingbirds is merely a matter of nutrition, in its ordinarily accepted sense. In a moulting bird, for example, there may be hundreds of feathers in process of growth at the same time, and feathers in all possible stages of development. If reduced nutrition is necessary for the formation of the downy portions of the feather, and still further reduction of nutrition for the formation of the quill, how can all of these processes of feather growth take place, through experiment or otherwise, *in the same individual at the same time*, as we know is the case in an actively moulting bird? Each feather has its definite function, and its predestined form and character, in accordance with its position on the bird's body; and feathers differ in character in different birds in accordance with their rôle in nature, depending upon whether they are owls, or swifts, or pigeons, or penguins, etc. Evidently the nutrition of the single feather and the nutrition of the individual bird are not necessarily one and the same thing; while defective or insufficient nutrition of the individual would leave its impress upon growing feathers, it is not likely that it would, in the case of a moulting bird, affect one phase or stage of feather growth without affecting all stages.

Each feather has its own cycle of growth, and the supply and quality of the nutrition for the perfection of its different parts must vary with each stage of growth, independently of degree of blood-pressure dependent upon food-supply. Hence we should not like to say that “The formation of the quill is probably the direct result of a progressive diminution of an already lessened food-supply,” but that it was due to the normally modified supply and character of the nutriment furnished by the blood-vessels to the feather at this particular and final stage of its

<sup>2</sup> Jones, Lynds. The Development of Nestling Feathers. Lab. Bull. No. 13, Oberlin College. Noticed in *The Auk*, January, 1907, p. 90.

growth; or that the answer to Mr. Riddles's question, "What causes the production of 'down'?" is to be found in malnutrition of the individual.

J. A. A.

#### VERTEBRATE PALEONTOLOGY

**New Fossil Mammals from Egypt.**—It was announced some time ago that the expedition of the American Museum of Natural History to the famous fossil beds of the Fayûm had been highly successful, and particulars of the results have been awaited with much interest. Professor Osborn has just issued a short paper<sup>1</sup> describing some of the more remarkable discoveries. Two new forms, unfortunately represented only by portions of the lower jaw, are so peculiar that their ordinal position remains uncertain. One of these is named *Ptolemaia lyonsi*, and is taken as the type of a new family Ptolemaiidae. It is even stated that it possibly represents a new order. The other, *Apidium phiomensis*, new genus and species, "was evidently a small omnivorous or frugivorous form with partly cuspidate teeth"; but at present its precise affinities are unknown. Two other fossils are described, representing new genera (*Phiomys* and *Metaphiomys*) of rodents, placed in the family Eomyidae.

T. D. A. C.

*Errata:* The title of the article by Professor George H. Parker in the September issue, p. 601, should read "The Origin of the Lateral Eyes of Vertebrates." The figure on p. 606 is inverted.

<sup>1</sup> *Bull. Am. Mus. N. Hist.*, XXIV, 265-272, March 25, 1908.

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